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THE DEVELOPMENT OF CLIMAX FORMATIONS IN NORTHERN MINNESOTA

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The climax vegetation of a region is the result of all the forces operative upon it during its development, its general features being determined by the climate. Within a region the same final or climax stage results through a series of developmental or successional stages, whether starting from open water, solid rock, or denuded land.

It is the purpose of this paper to trace the succession from the initial to the climax stage in northern Minnesota, as well as the forces that have operated together to produce the climax or earlier stages of stabilization. These processes may be expected to continue without change, unless disturbed by a reversal of climatic conditions or by any other change which would seriously affect the water or light relations of the dominants in the climax.

The results here presented are based upon field work which has extended over a period of four years and has involved the study of coniferous and deciduous forest, swamp, and other developmental stages in different parts of the state. The work has been of an exact nature, with quadrats and instruments, so that definite information has been obtained as to the structure of the climax associations and the successional stages leading up to them, as well as to the factors concerned in the development.

The work was undertaken at the suggestion and under the direction of Dr. Frederic E. Clements, to whom the writers are indebted for invaluable suggestions and criticisms, and particularly for his kindness in placing freely at their disposal the manuscript of his work on *Plant Succession,* which has been used in the preparation of this report. The classification of successions and of

the causes initiating them and leading up to the development of the climax formations, as well as the terminology used, are those proposed by Clements in *Plant Succession.*

Climax Formations

Minnesota may be divided into three great regions according to the final or climax vegetation which dominates them, viz., pine forest, deciduous forest, and prairie. The distribution of the three climax formations may be indicated by the accompanying map (figure 1).

Classification of Successions

It has been customary to classify successions according to the initial cause, but it has been pointed out by Clements (1916) that such a classification is unnatural and unsatisfactory, since the same climax type may result from several different initiating causes. Successions are accordingly classified as follows:

I. Primary Succession
   1. Hydrarch
   2. Xerarch

II. Secondary Succession

Whether a succession is to be primary or secondary is determined by the initial cause which, by the extent to which the habitat is disturbed, affects the kind and amount of water present. Primary succession may be subdivided into hydrarch and xerarch successions, depending upon the character of the initial stage. Those beginning in water are called hydrarch, those beginning in dry conditions, xerarch (Cooper 1912).

Course of Succession

The course of succession is indicated by the zonation peculiar to a region. Accordingly, the key to the order of succession and to the factors which have controlled it is to be found in the study of zonation and the existing conditions of the different zones, or their corresponding associes.

In tracing the development of the climax, the effect of the various causes of succession in producing new habitats is first considered briefly. In turn, the effect of the ecesic and stabilizing causes in determining the nature of the development to the final

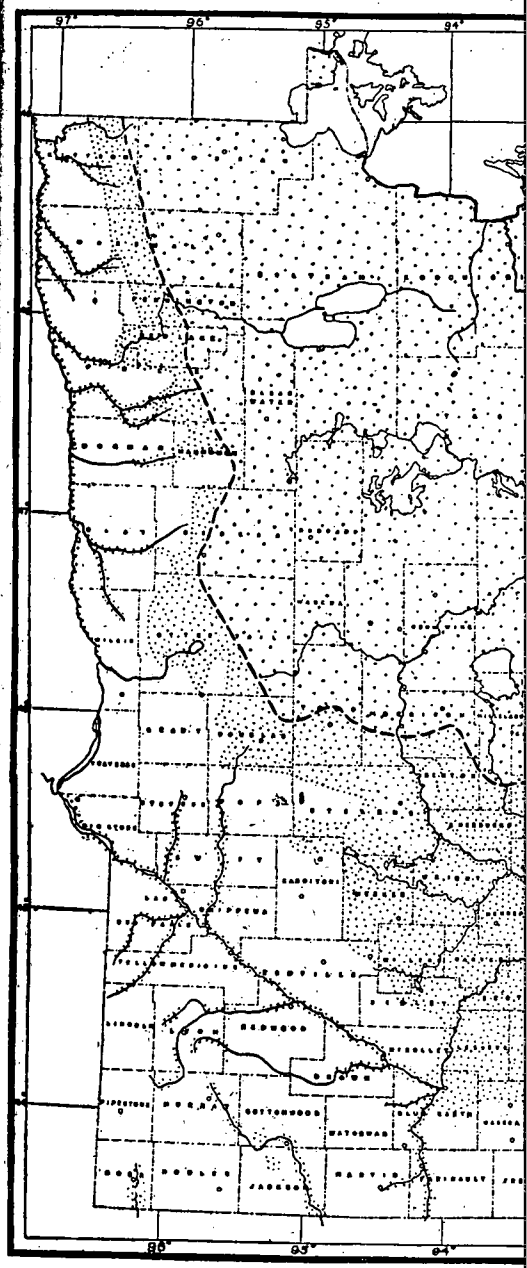

Fig. 1. Map of Minnesota showing distribution
produced from fig. 14, Bulletin No. 12, M

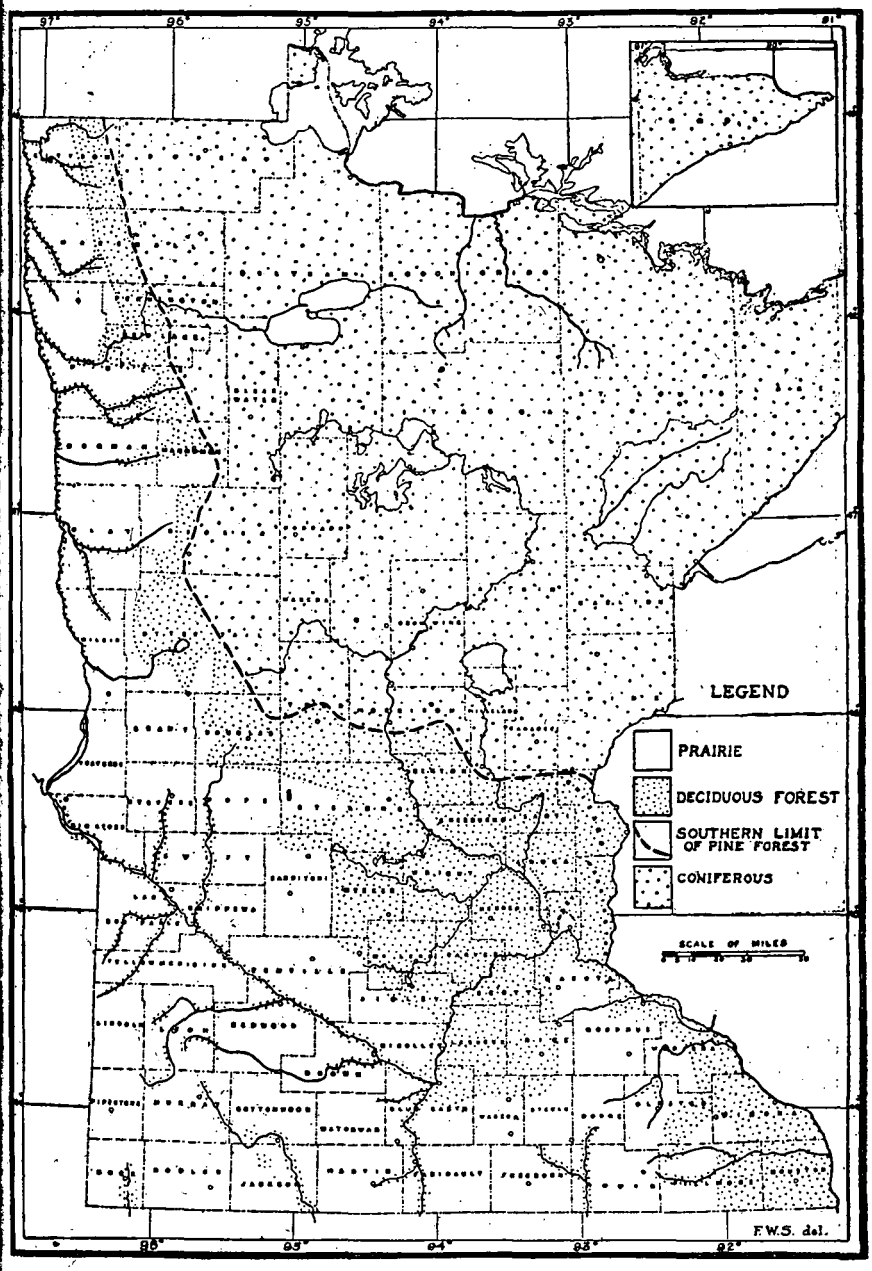

Fig. 1. Map of Minnesota showing distribution of climax formations. (Reproduced from fig. 14, Bulletin No. 12, Minnesota Geological Survey.)

climax for each of the principal successions in each of the climax associations will be discussed.

PINUS STROBUS-PINUS RESINOSA ASSOCIATION

I. Primary Succession

Initial causes: Wherever water collects in sufficient quantities to destroy completely any vegetation which may have existed previously in the area covered, a primary succession may begin. The lakes of Minnesota are largely due to glaciation, by which the drainage systems that had developed during the time from the Cretaceous period down to the glacial epoch were more or less completely blotted out, causing the development of new drainage channels. The deposition of glacial till on the retreat of the ice-sheet also blocked many of the drainage channels, causing the lower areas to become filled with water from the melting ice. Some of the lakes in northeastern Minnesota probably existed essentially in their present form before the glacial period, occupying the troughs of the central folds that have occurred in the earth's surface. Such lakes have rock-bound shores and are usually long, narrow, and deep. Owing to the hardness of the rocks forming their shores, they probably were little affected by the passage of the continental glacier.

The effects of climate as initial causes since the glacial period are of less consequence. The flooding of areas by man or by beavers would initiate a primary succession if the areas were flooded to sufficient depths. There is no evidence, however, that primary successions in Minnesota have been initiated by biotic agencies.

1. HYDRARCH SUCCESSION

This succession, which has its origin in water and culminates in the *Pinus strobus-P. resinosa* climax, shows a series of stages which may be indicated as follows:

(1) *Chara-Philotria* Associes
(2) *Castalia-Nymphaea* Associes
(3) *Scirpus-Zizania* Associes
(4) *Carex* Associes
(5) *Chamaedaphne-Andromeda* Associes
(6) *Larix-Picea* Associes
(7) *Abies-Betula* Associes
(8) *Pinus* Association

Variations of this sequence may som
sion or slight development of a stage, o
disappearance of one or more of its c
are indicated in the discussions of the
and will be more fully treated in a late

(1) *Chara-Philotria* A

This associes appears only in deep w
six to twenty feet. In such places succ
invasion of *Chara, Philotria,* and other
The character of the bottom plays a
plants. On sandy or muddy bottoms the
ily, but on coarse gravel or rock this is
northeastern Minnesota, which occur in
ingly devoid of submerged aquatics.

Consocies: *Chara* is the first species
and consequently in the deeper places is
ent. In somewhat shallower water, pe
feet, *Philotria canadensis* appears, and
cularia vulgaris, Ceratophyllum deme
Myriophyllum spicatum. This associes
water out to the *Castalia-Potomogeto*
Carex zone. The plants of this asso
but often form very dense masses of ve
to six feet of water, where they make t

Secondary species: Associated with
twelve feet in depth are: *Potamogeton*
zosteraefolius.

(2) *Castalia-Nymphae*

The principal natural causes contrib
this associes are: (1) the deposition of
and transported into the lake, filling it
associes are able to enter and establish
lation of decayed remains of the pionee
The latter cause works very slowly in
but is important in forming a substra
lishment of plants of the following asso
if not complete, would lower the wate
associes would find favorable condition

Variations of this sequence may sometimes occur by the omission or slight development of a stage, or within an associes by the disappearance of one or more of its consocies. Such variations are indicated in the discussions of the associes of the successions and will be more fully treated in a later report.

(1) *Chara-Philotria* Associes

This associes appears only in deep water, varying in depth from six to twenty feet. In such places succession may begin with the invasion of *Chara, Philotria,* and other dominants of the associes. The character of the bottom plays a part in the ecesis of these plants. On sandy or muddy bottoms they establish themselves readily, but on coarse gravel or rock this is not possible. The lakes of northeastern Minnesota, which occur in basins of rock, are accordingly devoid of submerged aquatics.

Consocies: *Chara* is the first species to invade the lake bottoms, and consequently in the deeper places is often the only species present. In somewhat shallower water, perhaps to a depth of fifteen feet, *Philotria canadensis* appears, and associated with it are *Utricularia vulgaris, Ceratophyllum demersum* and sometimes also *Myriophyllum spicatum.* This associes extends from the deeper water out to the *Castalia-Potomogeton* zone, or even out to the *Carex* zone. The plants of this associes are always submerged, but often form very dense masses of vegetation, particularly in two to six feet of water, where they make their most luxuriant growth.

Secondary species: Associated with them in water up to ten or twelve feet in depth are: *Potamogeton perfoliatus* and *Potamogeton zosteraefolius.*

(2) *Castalia-Nymphaea* Associes

The principal natural causes contributing to the development of this associes are: (1) the deposition of material eroded by streams and transported into the lake, filling it up until the species of the associes are able to enter and establish themselves, (2) the accumulation of decayed remains of the pioneer plants of the lake bottoms. The latter cause works very slowly in comparison with the former but is important in forming a substratum suitable for the establishment of plants of the following associes. Drainage of the lakes, if not complete, would lower the water-level so that plants of this associes would find favorable conditions for growth.

Consocies: Three species are typically found as dominants in this associes:

Castalia odorata — *Potamogeton natans*
Nymphaea advena

While these three species are generally associated, combinations of any two of them may occur, and in some instances only a single species is to be found representing the associes. These species grow in water from one to six feet in depth, the best development being in from three to six feet of water.

The following plants occur more or less abundantly as secondary species:

Ceratophyllum demersum	*Potamogeton pectinatus*
Myriophyllum spicatum	*Utricularia vulgaris*
Potamogeton perfoliatus	*Zannichellia palustris*

Polygonum amphibium and *Batrachium trichophyllum* occur occasionally in this zone, but never very abundantly. Among the other plants are to be found duckweeds floating on the surface in more or less abundance. The growth of waterlilies so that their leaves cover the surface of the water more or less completely greatly checks or prevents the development of submerged aquatics.

(3) *Scirpus-Zizania* Associes

The reaction of the plants of the *Castalia-Nymphaea* associes in retaining and binding into a soil the sedimentary material washed into the lake, as well as by accumulation of the decayed remains of the waterlilies and pondweeds, causes the lake shore to be built up more rapidly, thereby enabling *Scirpus, Zizania,* and other species of this associes to invade and become established.

The lowering of the water-level by partial drainage of a lake or by any other cause would result in the movement of the *Castalia-Nymphaea* zone out into deeper water and in its replacement by the *Scirpus-Zizania* zone, or if the lowering of the water-level were sufficient the latter would invade to the exclusion of the former.

Consocies: The associes consists of several dominants which may occur all together or in various combinations; or, in other instances, a single member may be the only representative in this stage of development. The typical consocies are:

Phragmites phragmites	*Typ*
Scirpus occidentalis	*Ziz*
Scirpus validus	

Equisetum fluviatile often occurs a restricted areas in this associes. It s bottom in a depth of one to three feet rather extensive areas of pure growth the mouth of Boy River and at the Ely. Usually, however, *Equisetum* cies of the associes.

The distribution of the consocies of the lake shore. *Scirpus* is able to sand or sandy gravel, and where the *Scirpus* is usually or often the only come established on a lake shore and or eight feet or water without be *Philotria* and *Castalia-Nymphaea* as sion. Lake shores of pure, packed s subject to heavy wave-action or to a On shores much exposed to wind-dri the ice masses are carried is sufficien pletely preventing the establishment o often forming an abrupt wall or bank

Zizania is able to establish itself o of a lake or river is covered with silt of decayed plant remains, and conse of lakes subject to much wave-action ice. This is true also of *Phragmite Phragmites* may become established because of the bottom or because of

Phragmites may be the first inva beyond a depth of two or three feet found along the south and west sho the west side of Little Winnebegosh River for a short distance above wh begoshish. It also occurs in abunda from the mouth of Rainy River to five feet of water, the maximum de

Secondary species: Various duck

Phragmites phragmites *Typha latifolia*
Scirpus occidentalis *Zizania aquatica*
Scirpus validus

Equisetum fluviatile often occurs as an exclusive dominant over restricted areas in this associes. It seems to thrive best on a silty bottom in a depth of one to three feet of water. In places it forms rather extensive areas of pure growth, notably on Leech Lake near the mouth of Boy River and at the west end of Long Lake near Ely. Usually, however, *Equisetum* occurs mixed with other species of the associes.

The distribution of the consocies depends upon the character of the lake shore. *Scirpus* is able to establish itself in well-packed sand or sandy gravel, and where the lake shore is of this character, *Scirpus* is usually or often the only member present. It may become established on a lake shore and extend out to a depth of six or eight feet or water without being preceded by the *Chara-Philotria* and *Castalia-Nymphaea* associes of the normal succession. Lake shores of pure, packed sand occur where the shore is subject to heavy wave-action or to a limited amount of ice-action. On shores much exposed to wind-driven ice, the force with which the ice masses are carried is sufficient to plow up the shore, completely preventing the establishment of *Scirpus* or other plants and often forming an abrupt wall or bank along the shore exposed.

Zizania is able to establish itself only where the shore or bottom of a lake or river is covered with silt or with a considerable amount of decayed plant remains, and consequently is not found in parts of lakes subject to much wave-action or to the action of wind-driven ice. This is true also of *Phragmites* and *Typha,* but apparently *Phragmites* may become established where *Zizania* can not, either because of the bottom or because of too much wave-action.

Phragmites may be the first invader in a lake, but usually not beyond a depth of two or three feet. Examples of this are to be found along the south and west shores of Ball Club Lake and on the west side of Little Winnebegoshish, and along the Mississippi River for a short distance above where it flows into Little Winnebegoshish. It also occurs in abundance in Lake of the Woods from the mouth of Rainy River to Oak Point, where it grows in five feet of water, the maximum depth observed.

Secondary species: Various duckweeds are to be found floating

on the surface, and as submerged plants different kinds of algae, as well as *Potamogeton, Myriophyllum, Utricularia, Batrachium,* etc., occur. The characteristic secondary species of this associes are the following:

Acorus calamus	*Polygonum amphibium*
Alisma plantago-aquatica	*Sagittaria arifolia*
Eleocharis palustris	*Sagittaria latifolia*
Naumburgia thyrsiflora	*Sparganium eurycarpum*

The last two named are never abundant, but are usually represented by a few individuals. *Naumburgia* becomes more abundant in the following associes.

(4) *Carex* Associes

The reaction of the plants of the *Scirpus-Zizania* associes in building up the lake shores, by retaining the sedimentary material washed into the lake and by the accumulation of decayed plant remains, results in a lowering of the water-level. This permits the invasion and establishment of species of *Carex,* which are the dominants of this associes. The lowering of the water-level of the lake by drainage or by any other cause would bring about a change of conditions favorable for the establishment of plants of this associes.

Consocies: Several species of *Carex* are the dominants of this stage. The following are the typical species:

Carex aquatilis	*Carex trichocarpa*
Carex filiformis	

Carex aquatilis and *C. filiformis* are less abundant than *C. trichocarpa,* although in some places *C. filiformis* occurs exclusively. Usually the *Carex* zone is narrow, varying from three or four feet to thirty or forty, although in exceptional cases it may be much wider. In many instances the *Scirpus-Zizania* associes is poorly developed, being represented by a sparse growth of *Zizania* or of *Zizania* and *Scirpus,* or it may be entirely absent, the *Carex* associes directly following the *Castalia-Nymphaea* associes. The sedges push out farther into the water from year to year by the development of rootstocks and cause a rapid filling of the lake, thus enabling the following associes to become established.

Secondary species: The following species of sedges and grasses are usually present, but with the exception of *Carex diandra* never

appear in sufficient number to be regard
be true of *Carex diandra* in some cases

Carex bebbii	*Carex*
Carex diandra	*Phal*

The following species of herbs are c

Alsine longifolia	*Galiu*
Aster paniculatus	*Ment*
Campanula aparinoides	*Naum*
Cicuta bulbifera	*Rum*
Dryopteris thelypteris	*Scut*

Galium, Campanula and *Alsine* form
sedges and grasses, and often make ve
larly the first two.

The following species often occur
usually not present in great number:

Asclepias incarnata	*Eupa*
Caltha palustris	*Iris*
Carduus muticus	*Lath*
Comarum palustre	*Men*
Epilobium lineare	*Poly*
Equisetum fluviatile	*Rum*
Eriophorum angustifolium	

(5) *Chamaedaphne-Andro*

The appearance of *Sphagnum* in p
tufts of *Carex* is made possible by th
builds a substratum at or above the wat
Sphagnum then colonizes about the clu
shallow water between tufts. Althoug
often been observed to invade open wa
to occur in Minnesota. The replacem
the bog heaths is usually attributed to
the water owing to the presence of *Sp*
observations in numerous swamps it se
ficient increase in acidity to account fo
this time to state the cause of the repla
num and species of bog heaths, but in s
Carex stage is unfavorable to its conti

appear in sufficient number to be regarded as consocies. This may be true of *Carex diandra* in some cases.

Carex bebbii	*Carex sartwellii*
Carex diandra	*Phalaris arundinacea*

The following species of herbs are characteristic:

Alsine longifolia	*Galium trifidum*
Aster paniculatus	*Mentha canadensis*
Campanula aparinoides	*Naumburgia thrysiflora*
Cicuta bulbifera	*Rumex britannica*
Dryopteris thelypteris	*Scutellaria galericulata*

Galium, Campanula and *Alsine* form a ground layer under the sedges and grasses, and often make very dense growths, particularly the first two.

The following species often occur with this associes, but are usually not present in great number:

Asclepias incarnata	*Eupatorium purpureum*
Caltha palustris	*Iris versicolor*
Carduus muticus	*Lathyrus palustris*
Comarum palustre	*Menyanthes trifoliata*
Epilobium lineare	*Polygonum amphibium*
Equisetum fluviatile	*Rumex occidentalis*
Eriophorum angustifolium	

(5) *Chamaedaphne-Andromeda* Associes

The appearance of *Sphagnum* in pools of water between the tufts of *Carex* is made possible by the advancing *Carex* which builds a substratum at or above the water-level of the lake or pond. *Sphagnum* then colonizes about the clumps of *Carex* or in pools of shallow water between tufts. Although in Europe *Sphagnum* has often been observed to invade open water this has not been found to occur in Minnesota. The replacement of the *Carex* stage by the bog heaths is usually attributed to an increase in the acidity of the water owing to the presence of *Sphagnum,* but from repeated observations in numerous swamps it seems that there is not a sufficient increase in acidity to account for this. It is not possible at this time to state the cause of the replacement of *Carex* by *Sphagnum* and species of bog heaths, but in some way the reaction of the *Carex* stage is unfavorable to its continuance while it is distinctly

favorable to the development of *Sphagnum*. The appearance of *Sphagnum* provides conditions suitable for the invasion of *Andromeda, Ledum* and others of this associes.

Consocies: The following plants are the typical dominants: *Chamaedaphne calyculata, Andromeda glaucophylla* and *Ledum groenlandicum*. *Andromeda* and *Chamaedaphne* make thir appearance very soon after *Sphagnum,* so that before the latter has completely occupied the area, the bog heaths have appeared. By the time that *Sphagnum* has formed a complete zone, the bog heaths are usually well-established throughout the *Sphagnum* zone.

In the fully developed associes, *Ledum groenlandicum* usually appears as one of the dominants, but in some instances it does not occur at all. When *Ledum* does appear, it is at a later stage than the other two. *Kalmia glauca* is sometimes present, but hardly in sufficient quantity to be called a consocies. It is abundant northward, and occurs rarely in other places. Either *Chamaedaphne* or *Andromeda* may be the first successor of the pioneer *Sphagnum,* or both may appear at essentially the same time.

A few cases have been observed where *Salix candida, S. myrtilloides, S. petiolaris* and *Betula pumila* were the first invaders of the *Carex* associes, to be followed by the development of *Sphagnum* and soon afterward by *Ledum*. It seems rather probable, however, that this is a disturbance of the normal primary sequence due to a partial secondary succession initiated by lumbering or flooding.

Secondary species: Along with *Andromeda* and *Chamaedaphne,* on the hummocks of *Sphagnum,* is usually to be found a more or less extensive development of *Oxycoccus macrocarpus* and *O. oxycoccus*. The *Chamaedaphne-Andromeda* associes is further marked by the presence of very characteristic herbs, among which *Sarracenia purpurea, Drosera rotundifolia,* and *Smilacina trifolia* are most typical. *Saxifraga pennsylvanica, Eriophorum augustifolium* and *E. gracile* are sometimes found. *Menyanthes, Comarum* and others of the preceding *Carex* associes occur also.

(6) *Larix-Picea* Associes

The formation of *Sphagnum* mounds builds up the substratum above the water-level and provides for better aeration, and thus furnishes suitable conditions for the invasion of *Larix* and *Picea,* which become established, and finally form such a dense growth that the *Chamaedaphne-Andromeda* associes disappears completely.

Consocies: There are two trees th
in this associes, viz., *Larix laricina* an
Larix is the first invader of the
scrub, and in some cases may be the s
a more or less indefinite zone of *Pi*
swamp. *Larix* ranges farther to the
latter is less abundant as the southe
proached. Usually *Larix* and *Picea* ar
Picea becomes more abundant and repl
pletely.

When *Larix* is the most abundan
dense, and the smaller reduction of th
the shrubs of the *Chamaedaphne-And*
long as *Larix* remains the dominant.
daphne disappear first, as they are u
Ledum may persist as long as the swa

When the bog becomes filled up wi
and rotted wood, or filled around the
soil from the sides, *Picea* and *Thuja* m
When they become more numerous tha
of the *Chamaedaphne-Andromeda* asso
cession advances to the next stage.

If very extensive areas are occupied
sist indefinitely as a subclimax, owing
changes take place that would make po
lishment of species of the following
natural development may be retarded
may be accelerated by draining.

Secondary species: In addition to
and *Ledum,* which belong typically to
sist in the *Larix-Picea* associes, the f
istic shrubs of this associes: *Ribes huds*
alnifolia and *Lonicera oblongifolia*. M
in the *Chamaedaphne-Andromeda* asso
this stage. Others are characteristic
regular sequence of stages they appear
find their best development here. Th
hummocks of living *Sphagnum*:

Drosera rotundifolia *Mite*
Eriophorum gracile *Oxy*

Consocies: There are two trees that are the typical dominants in this associes, viz., *Larix laricina* and *Picea mariana.*

Larix is the first invader of the *Chamaedaphne-Andromeda* scrub, and in some cases may be the sole representative, except for a more or less indefinite zone of *Picea* along the border of the swamp. *Larix* ranges farther to the south than *Picea,* so that the latter is less abundant as the southern limit of its range is approached. Usually *Larix* and *Picea* are intermingled, or sometimes *Picea* becomes more abundant and replaces *Larix* more or less completely.

When *Larix* is the most abundant species, the growth is less dense, and the smaller reduction of the light intensity may enable the shrubs of the *Chamaedaphne-Andromeda* associes to persist as long as *Larix* remains the dominant. *Andromeda* and *Chamaedaphne* disappear first, as they are unable to endure shading, but *Ledum* may persist as long as the swamp itself remains.

When the bog becomes filled up with partly decayed *Sphagnum* and rotted wood, or filled around the edges by the washing-in of soil from the sides, *Picea* and *Thuja* may replace *Larix* completely. When they become more numerous than the tamaracks, the shrubs of the *Chamaedaphne-Andromeda* associes disappear, and the succession advances to the next stage.

If very extensive areas are occupied by this associes, it may persist indefinitely as a subclimax, owing to the slowness with which changes take place that would make possible the invasion and establishment of species of the following *Abies-Betula* associes. The natural development may be retarded by burning or lumbering, or may be accelerated by draining.

Secondary species: In addition to *Andromeda, Chamaedaphne,* and *Ledum,* which belong typically to the preceding stage but persist in the *Larix-Picea* associes, the following occur as characteristic shrubs of this associes: *Ribes hudsonianum, R. triste, Rhamnus alnifolia* and *Lonicera oblongifolia.* Many of the herbs which occur in the *Chamaedaphne-Andromeda* associes are still to be found in this stage. Others are characteristic of this associes, since in a regular sequence of stages they appear here for the first time and find their best development here. The following herbs occur on hummocks of living *Sphagnum*:

Drosera rotundifolia	*Mitella nuda*
Eriophorum gracile	*Oxycoccus oxycoccus*

Sarracenia purpurea	*Smilacina trifolia*
Saxifraga pennsylvanica	*Viola renifolia* var. *brainerdii*

With the exception of *Mitella* and *Viola*, the plants of the above list are relicts of the preceding associes. With these species may also be found:

Carex gynocrates	*Carex trisperma*
Carex leptalea	*Coptis trifolia*
Carex paupercula pallens	*Habenaria dilatata*
Carex scirpoides	*Habenaria hyperborea*
Carex tenella	*Habenaria obtusata*

Where *Sphagnum* has died out leaving mounds of humus, and along the border of the swamp where filling-up has resulted in the death of *Sphagnum*, the following plants are characteristic:

Carex tenella	*Linnaea borealis*
Carex trisperma	*Maianthemum canadense*
Chiogenes hispidula	*Osmunda cinnamomea*
Clintonia borealis	*Osmunda claytoniana*
Coptis trifolia	*Petasites palmata*
Cornus canadensis	*Pyrola asarifolia*
Cypripedium hirsutum	*Pyrola secunda*
Cypripedium parviflorum	*Trientalis americana*
Dryopteris cristata	

Chiogenes and *Linnaea* are found often on decayed fallen logs, where they usually form a dense mat over the surface. Many of the plants of the above list are to be found typically on swamp borders. *Gaultheria procumbens* has been found occasionally with the above plants.

(7) *Abies-Betula* Associes

The filling-up of a swamp by the washing-in of soil from the sides and in part also by the accumulation and subsequent decay of *Sphagnum* and other plant remains results in the formation of a soil rich in humus, but one in which the water-content is much reduced as compared with that of the substratum of the *Larix-Picea* or *Chamaedaphne-Andromeda* associes. The formation of humus and reduction of water-content favors the invasion and establishment of the plants of the *Abies-Betula* associes. Drainage of a swamp would accelerate the appearance of subsequent stages.

Consocies: The following are the us
samea, Betula papyrifera, B. lutea, Pic
occidentalis.

All of these are not found together i
but in the stage of development from s
the finally dominant pines, combination
these may occur. By aggregation, famil
of the above may occur and are frequ
dominance of any of them is rare.

Secondary species: Characteristic u
are:

Acer spicatum	*Rham*
Alnus incana	*Rhus*
Cornus stolonifera	*Ribes*
Corylus rostrata	*Ribes*
Lonicera hirsuta	*Ribes*
Lonicera oblongifolia	*Rosa*
Parthenocissus quinquefolia	*Vibur*
Prunus pennsylvanica	*Vibur*
Prunus virginiana	

Semi-woody plants such as *Diervilla l*
are usually present.

Amelanchier oblongifolia and *Sorbus*
ally. *Lonicera oblongifolia* and the last t
from the preceding associes, or from it
Abies-Betula associes. In some places
acicularis.

The following herbs are commonly

Aralia nudicaulis	*Equis*
Carex tenella	*Galiu*
Carex trisperma	*Maia*
Clintonia borealis	*Mitell*
Cornus canadensis	*Rubus*
Dryopteris cristata	*Strep*
Dryopteris phegopteris	*Trien*

Occasional plants of *Actaea rubra* ma

(8) *Pinus* Associa

The further filling of a swamp by th

Consocies: The following are the usual dominants: *Abies balsamea, Betula papyrifera, B. lutea, Picea canadensis* and *Thuja occidentalis.*

All of these are not found together in any given area or zone, but in the stage of development from spruce-tamarack swamps to the finally dominant pines, combinations of any two or more of these may occur. By aggregation, families or colonies of any one of the above may occur and are frequently encountered. Pure dominance of any of them is rare.

Secondary species: Characteristic undershrubs of this associes are:

Acer spicatum	*Rhamnus alnifolia*
Alnus incana	*Rhus rydbergii*
Cornus stolonifera	*Ribes floridum*
Corylus rostrata	*Ribes hudsonianum*
Lonicera hirsuta	*Ribes prostratum*
Lonicera oblongifolia	*Rosa acicularis*
Parthenocissus quinquefolia	*Viburnum lentago*
Prunus pennsylvanica	*Viburnum pubescens*
Prunus virginiana	

Semi-woody plants such as *Diervilla lonicera* and *Rubus triflorus* are usually present.

Amelanchier oblongifolia and *Sorbus americana* occur occasionally. *Lonicera oblongifolia* and the last two species of *Ribes* persist from the preceding associes, or from it may invade the adjacent *Abies-Betula* associes. In some places *Rosa blanda* replaces *R. acicularis.*

The following herbs are commonly found:

Aralia nudicaulis	*Equisetum sylvaticum*
Carex tenella	*Galium triflorum*
Carex trisperma	*Maianthemum canadense*
Clintonia borealis	*Mitella nuda*
Cornus canadensis	*Rubus triflorus*
Dryopteris cristata	*Streptopus roseus*
Dryopteris phegopteris	*Trientalis americana*

Occasional plants of *Actaea rubra* may be found with the above.

(8) *Pinus* Association

The further filling of a swamp by the carrying-in of soil from

the sides and by the accumulation of decayed plant-remains brings about a reduction of the water-content of the soil. The habitat has now become completely mesophytic in character. The reduction of the water-content and the ability of pine seedlings to grow in a reduced light makes it possible for pines to invade and to become established. The actual invasion of the *Abies-Betula* zone must occur in the spaces between more widely separated individuals of that zone. The destruction of members of the *Abies-Betula* associes by diseases, insects, and the breaking and uprooting of trees by wind, all contribute to the formation of openings in which pines may invade and establish themselves. The greater longevity of pines as compared with *Abies, Betula* and *Picea* enables the pines to become dominant in competition with them.

Consocies: The dominant species of pines of the climax forest are *P. strobus* and *P. resinosa*. The two species often occur in a mixture, or extensive tracts may be occupied by either as a pure dominant. It seems probable that *P. strobus* would finally replace *P. resinosa*, but at present this cannot be confirmed.

Secondary species: Shrubs are usually absent in the well-developed climax. The following low shrubs and herbs are the characteristic plants of the usually sparse ground layer:

Anemone quinquefolia
Chimaphila umbellata
Cornus canadensis
Diervilla lonicera
Gaultheria procumbens
Lycopodium obscurum
Maianthemum canadense
Pyrola americana
Pyrola secunda
Vaccinium canadense
Vaccinium pennsylvanicum

Antennaria canadensis, Lycopodium annotinum and *Pyrola elliptica* occur occasionally. In many places the growth of pines is so dense that the ground is practically bare of vegetation, only scattering plants being found. In such places the ground is well carpeted with pine needles. This, probably, represents the typical condition of the climax pine forest, the presence of an abundance of herbs being due to a disturbance of typical conditions by passage of fire through the forest.

2. XERARCH SUCCESSION

Initial causes: A xerarch succession is one originating in a dry habitat. Such a habitat is to be found in Minnesota only in

areas where the surface is of solid rock
deficiency in water-content. The most e
in northeastern Minnesota, comprising nea
to twenty-five miles wide along the northe
from the eastern boundary of Koochich
rior. Smaller areas occur in the north
parts of the state. The rocks of northe
nesota are probably of igneous origin a
period. They consist of greenstones, qu
schists, and jasper variously intermingl
have remained at the surface since the
other parts of the state the rocks of tha
by sedimentary formations of subsequen
the glaciers during the Glacial period
rocks somewhat and left deposits of gla
but extensive areas still remain exposed.
areas for the initiation of xerarch succe

Weathering of the exposed rock sur
development of vegetation within that
rocks are still as smooth as they were l
and polished by glacial action, and on t
is to be found. On others the surface
tegrated by weathering, in places to a d
in such places a dense covering of veget

A succession having its origin on r
Pinus association also shows a series o
stages of xerarch succession, however, a
those of the hydrarch and complete data
the available data of quadrats, transects
seem to be as follows:

(1) Crustose Lichen Associes
(2) *Cladonia-Polytrichum* Associes
(3) Herbaceous Associes
(4) *Juniperus* Associes
(5) *Pinus-Betula* Associes
(6) *Pinus* Association.

(1) Crustose Lichen

Crustose lichens alone are able to ga
rock, owing to the extreme deficiency
to which they are subjected. Since the

areas where the surface is of solid rock, representing an extreme deficiency in water-content. The most extensive area of this kind is in northeastern Minnesota, comprising nearly all of an area twenty to twenty-five miles wide along the northern boundary and extending from the eastern boundary of Koochiching county to Lake Superior. Smaller areas occur in the northeastern and southeastern parts of the state. The rocks of northern and northeastern Minnesota are probably of igneous origin and belong to the Archean period. They consist of greenstones, quartzites, granites, gneisses, schists, and jasper variously intermingled. These Archean rocks have remained at the surface since the Archean period, while in other parts of the state the rocks of that period have been covered by sedimentary formations of subsequent periods. The passage of the glaciers during the Glacial period planed down the Archean rocks somewhat and left deposits of glacial till over some of them, but extensive areas still remain exposed. These constitute the bare areas for the initiation of xerarch succession.

Weathering of the exposed rock surface has contributed to the development of vegetation within that area. In some places the rocks are still as smooth as they were left after being worn down and polished by glacial action, and on these little or no vegetation is to be found. On others the surface of the rock has been disintegrated by weathering, in places to a depth of several inches, and in such places a dense covering of vegetation has developed.

A succession having its origin on rock and culminating in the *Pinus* association also shows a series of progressive stages. The stages of xerarch succession, however, are not as readily traced as those of the hydrarch and complete data are not yet at hand. From the available data of quadrats, transects, and field notes, the stages seem to be as follows:

(1) Crustose Lichen Associes
(2) *Cladonia-Polytrichum* Associes
(3) Herbaceous Associes
(4) *Juniperus* Associes
(5) *Pinus-Betula* Associes
(6) *Pinus* Association.

(1) Crustose Lichen Associes

Crustose lichens alone are able to gain a foothold on bare hard rock, owing to the extreme deficiency of water and the exposure to which they are subjected. Since they are able to grow during

periods of wet weather and to remain in a state of desiccation for an indefinite time between periods favorable for growth, the conditions which are too adverse for other forms of plant life permit at least a certain amount of growth of lichen pioneers. "The crustaceous lichens furnish most of the species which first gain a footing on the rocks, and of these were found three or four species of *Placodium,* a half dozen or more *Lecanoras* as well as a large number of *Biatoras, Lecideas* and *Buellias.* Of the foliaceous lichens the *Umbilicarias* are most characteristically rock pioneers." (Fink, 1899 : 221.) These might grow for hundreds of years before the establishment of any other plant form in that area. Rock surfaces may be found now which have not advanced beyond the crustose lichen stage, but it is not possible to say how soon or how long after the glacial period the invasion of such surfaces by the lichens began. A long-continued growth of crustose lichens on a rock surface, however, would tend to favor the invasion and establishment of other forms of plant life.

The formation of pools of water, even very small ones and of short duration, in shallow depressions of the rock surface, would provide a place to which algae and aquatic mosses might be carried and grow. This might happen repeatedly in the same place and would in time result in the accumulation of humus, and with the erosion of the rocks produce a small amount of soil in which other forms of plants could grow. Even without the invasion of algae or mosses, the accumulation of water in pools would carry in particles of rock that may have been loosened as the result of weathering, and in this way a small amount of soil be formed for the invasion of plants.

That algae and mosses may be carried to and live in pools of water on a solid rock surface can not be doubted. MacMillan (1898 : 1017) mentions the occurrence on Windigo Island in Lake of the Woods of *Sphagnum cymbifolium* forming miniature peat bogs, of two or three feet in extent and two and a half inches deep, upon high wind-swept rocks.

When pools of water are invaded by aquatics, it results in the development of a miniature hydrarch succession. That this is true is readily apparent from the instance above cited. When such pools are of short duration, the hydrarch succession is so short that it may be neglected.

(2) *Cladonia-Polytrich*

The formation of soil in slight a weathering and erosion of the rock su cess is aided by the action of the cr erode the rock surface and to loosen disintegration of the rock and the adc cay of lichens increases the water-co This increase in the water-content ma of larger lichens, such as *Cladonia,* a

Consocies: The plants typically are *Cladonia gracilis, C. rangiferina* One of the first lichens to appear afte *naria microphylla,* which may someti but usually appears in more or less d foliose *Peltigeras* and the fruticose C pear, commonly occurring with *Polytr*

Among the *Cladonias, C. gracilis,* are most abundant in open and mo *ferina* may occur also in open places uriance of growth which is characte spots. The appearance of a few shr furnishes some protection from the wind, enabling *C. rangiferina* to ma the appearance of the shrubs.

These sometimes occur only in d disintegrated particles of rock are ca rain, and such places are accordingly t are suitable for the development of C other places these plants form very e surface, often to a depth of several i

Secondary species: Other species *melia, Umbilicaria* and a few small m

(3) HERBACEOUS

The further disintegration of rock by the action of lichens and mosses a from their decay, forms a soil layer over the surface of the rock. The and the increase in water-holding capa both work together to make condition

(2) *Cladonia-Polytrichum* ASSOCIES

The formation of soil in slight amounts takes place by the weathering and erosion of the rock surface. The weathering process is aided by the action of the crustose lichens which tend to erode the rock surface and to loosen particles of the rock. The disintegration of the rock and the addition of humus from the decay of lichens increases the water-content of the soil so formed. This increase in the water-content makes possible the establishment of larger lichens, such as *Cladonia,* and mosses.

Consocies: The plants typically represented in this associes are *Cladonia gracilis, C. rangiferina* and *Polytrichum commune.* One of the first lichens to appear after the crustose lichens is *Pannaria microphylla,* which may sometimes grow on quite firm rock but usually appears in more or less disintegrated areas. The large foliose *Peltigeras* and the fruticose *Cladonias* are the next to appear, commonly occurring with *Polytrichum.*

Among the *Cladonias, C. gracilis, C. fimbriata,* and such forms are most abundant in open and more exposed places. *C. rangiferina* may occur also in open places, but does not show the luxuriance of growth which is characteristic of it in more sheltered spots. The appearance of a few shrubs in crevices and pockets furnishes some protection from the sun and drying action of the wind, enabling *C. rangiferina* to make much better growth after the appearance of the shrubs.

These sometimes occur only in depressions in the rocks, since disintegrated particles of rock are carried into the depressions by rain, and such places are accordingly the only ones where conditions are suitable for the development of *Cladonia* and *Polytrichum.* In other places these plants form very extensive patches over the rock surface, often to a depth of several inches.

Secondary species: Other species of *Cladonia, Peltigera, Parmelia, Umbilicaria* and a few small mosses occur with the consocies.

(3) HERBACEOUS ASSOCIES

The further disintegration of rock surface by weathering, aided by the action of lichens and mosses and by the addition of humus from their decay, forms a soil layer of greater or lesser thickness over the surface of the rock. The increase in the depth of soil and the increase in water-holding capacity by the addition of humus both work together to make conditions suitable for the invasion of

grasses and other herbaceous plants.

Consocies: This associes shows no dominance of any single species of plants or even of a few species. Various species of grasses and herbs are to be found, but these are either scattered or a given species may show dominance over a very small area, i. e., by aggregation, it may form a family.

The following are the more representative plants of this stage:

Agrostis hiemalis	*Houstonia purpurea*
Arabis hirsuta	*Muhlenbergia racemosa*
Capnoides sempervirens	*Oryzopsis asperifolia*
Chamaenerion angustifolium	*Panicum xanthophysum*
Diervilla lonicera	*Potentilla tridentata*
Euthamia graminifolia	*Solidago canadensis*
Heuchera americana	*Solidago nemoralis*
Hieracium umbellatum	

Polypodium vulgare, Pellaea atropurpurea, and *Dryopteris thelypteris* are found sometimes, especially in crevices. A large number of other plants might be named, since nearly all the plants of the region may grow in crevices and in pockets filled with soil.

(4) *Juniperus* Associes

The presence of the herbaceous associes, since it is usually poorly developed, does not have a very evident reaction on the habitat in making it more favorable for the incoming shrubs. However, clumps of grass and herbs might be of some value in protecting the young seedlings of shrubs from the intense light and heat of the sun, and thereby enable them to obtain a footing.

Consocies: *Juniperus communis* and *Juniperus horizontalis* are the only dominants of this associes. Of these *J. communis* is the more abundant, often covering considerable areas.

Secondary species: *Taxus minor* occurs, but only occasionally. Many small deciduous shrubs are to be found also, the following being the most abundant:

Corylus americana	*Symphoricarpos racemosus*
Diervilla lonicera	*Vaccinium canadense*
Rhus rydbergii	*Vaccinium pennsylvanicum*
Rosa acicularis	

(5) *Pinus-Betula*

The intensely xerophytic condition deficiency in water-content and to the it is exposed in the bare rock condition, ually by continual weathering and by th result of the decay of the pioneer liche sive developmental stages. Thus by the its appearance, a considerable depth of the water-holding capacity of the soil h by the addition of humus. The habitat phytism has approached to a mesoph certain forms, at least, of trees. The *Juniperus* associes further favors the es tecting the young seedlings from too i by preventing evaporation from the soil

Consocies: The consocies are *Bet divaricata.* These may be intermixed, sive dominant within small areas. Alt pear dense when observed at a distance the fact that the plants are rather scat crevices and in depressions where rapidly.

Secondary species: Both species o definitely after the appearance of *Betu* cupying places less suitable for birches ter do not shade them too much. Othe when partly shaded make their appe *Betula* and *Pinus.* The shrubs found associes are:

Alnus crispa	*Prun*
Corylus rostrata	*Rhus*
Diervilla lonicera	*Rosa*
Prunus pennsylvanica	*Rubu*

In addition to plants from the prec shade-loving plants are to be found gro pines. The more characteristic species

Actaea rubra	*Corn*
Aralia nudicaulis	*Frag*

Pine-Birch

(5) *Pinus-Betula* ASSOCIES

The intensely xerophytic condition of the habitat, due to the deficiency in water-content and to the great evaporation to which it is exposed in the bare rock condition, has been ameliorated gradually by continual weathering and by the addition of humus as the result of the decay of the pioneer lichens and plants of the successive developmental stages. Thus by the time that *Juniperus* makes its appearance, a considerable depth of soil has been formed and the water-holding capacity of the soil has been increased markedly by the addition of humus. The habitat starting from intense xerophytism has approached to a mesophytic condition suitable for certain forms, at least, of trees. The presence of shrubs of the *Juniperus* associes further favors the establishment of trees by protecting the young seedlings from too intense evaporation and also by preventing evaporation from the soil in which they grow.

Consocies: The consocies are *Betula papyrifera* and *Pinus divaricata*. These may be intermixed, or either may be an exclusive dominant within small areas. Although the growth may appear dense when observed at a distance, a closer inspection reveals the fact that the plants are rather scattered, appearing only along crevices and in depressions where soil has accumulated more rapidly.

Secondary species: Both species of *Juniperus* may persist indefinitely after the appearance of *Betula* and *Pinus divaricata,* occupying places less suitable for birches and pines or where the latter do not shade them too much. Other shrubs which grow better when partly shaded make their appearance with the advent of *Betula* and *Pinus*. The shrubs found most abundantly with this associes are:

Alnus crispa	*Prunus virginiana*
Corylus rostrata	*Rhus rydbergii*
Diervilla lonicera	*Rosa acicularis*
Prunus pennsylvanica	*Rubus strigosus*

In addition to plants from the preceding associes, many of the shade-loving plants are to be found growing under the birches and pines. The more characteristic species are the following:

Actaea rubra	*Cornus canadensis*
Aralia nudicaulis	*Fragaria virginiana*

Galium boreale	*Maianthemum canadense*
Galium triflorum	*Pteris aquilina*
Lactuca canadensis	

In places where a few individuals of *P. divaricata* are grouped, the ground may be shaded to such an extent that very few plants are able to grow there. Patches of rock covered by *Cladonia rangiferina, C. gracilis,* other *Cladonias, Peltigera* and *Polytrichum,* or rocks with crustose lichens only are commonly to be found in the spaces between the tree growths.

(6) *Pinus* Association

The appearance of the *Juniperus* associes and the subsequent *Betula-Pinus* associes brings about a more rapid accumulation of humus, due to the increase in the number and size of individuals able to inhabit the area. The weathering processes still continue to break down the rocks and increase the amount of soil. All changes, accordingly, work to bring the habitat to more nearly mesophytic conditions. In the spaces between birch and jack pines and more or less shaded and protected by them, the invading pines of the *Pinus* association find suitable conditions for development.

Consocies: The dominants of the climax forest here as in the hydrarch succession are two species of pines, *P. resinosa* and *P. strobus.* No difference is to be found in the climax of the xerarch succession as compared with that of the hydrarch, except that the presence of certain secondary species may indicate along which line the succession has come.

Secondary species: As undershrubs of this associes are found:

Corylus rostrata	*Rosa acicularis*
Diervilla lonicera	*Rubus strigosus*
Lonicera hirsuta	*Vaccinium canadense*
Prunus pennsylvanica	*Vaccinium pennsylvanicum*
Prunus virginiana	

The presence of patches of bare rock or of lichen-covered rock, which have persisted throughout the stages leading up to the climax, reduces the completeness of dominance somewhat, and allows more under-vegetation than might otherwise be possible. The herbaceous layer consists of *Aralia, Cornus, Maianthemum, Chimaphila* and *Pyrola* as characteristic species. The fact that in an area of even a few acres, hydrarch and xerarch succession occur side by

side and, further, that these have b
velopment, perhaps repeatedly, mak
surance whether certain species are
mary succession or whether they hav
initiation of more or less extensive
ever this may be, the general sequer
seems quite clear.

II. Secondary S

Initial Causes: Any cause that
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Secondary succession may begin
stage and before the climax. The
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is affected by the disturbance of the
sion may be a very local one, such a
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of hundreds of square miles. In
of the habitat is apt to be affected
cause the secondary succession to be
Secondary successions may be class

1. Flood succession
2. Burn or clearing successio

1. THE FLOOD S

As indicated by the name, this i
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Minnesota are man and beavers. T
restricted area or over an extensiv
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primary succession beginning with
associes as already described (page

In making reservoirs of Gull, L

side and, further, that these have been disturbed during their development, perhaps repeatedly, makes it difficult to state with assurance whether certain species are characteristic of normal primary succession or whether they have appeared as the result of the initiation of more or less extensive secondary succession. However this may be, the general sequence of events in the succession seems quite clear.

II. Secondary Succession

Initial Causes: Any cause that destroys the existing vegetation of an area may initiate a secondary succession. Such causes may be changes in the physiography of a region, climatic or edaphic changes, or changes resulting from the action of biotic agents. None but biotic agents regularly cause secondary successions in Minnesota, except to the extent that forest fires, for example, may be shown to have been started by lightning.

Secondary succession may begin at any point after the pioneer stage and before the climax. The point at which the succession does begin is determined by the extent to which the water-content is affected by the disturbance of the habitat. A secondary succession may be a very local one, such as might be produced by a windthrow or by the formation of a small pond, or it may cover an area of hundreds of square miles. In a large area the water-content of the habitat is apt to be affected more profoundly, which would cause the secondary succession to begin at an earlier or lower stage. Secondary successions may be classified as follows:

1. Flood succession
2. Burn or clearing succession

1. THE FLOOD SUCCESSION

As indicated by the name, this is a succession due to the flooding of an area from any cause whatsoever. The two principal agents in causing secondary succession by flooding in northern Minnesota are man and beavers. The flooding may be over a very restricted area or over an extensive one, in either case causing a more or less complete hydrarch succession. If over an extensive area, the depth of water is apt to become sufficient to initiate a primary succession beginning with *Chara* and other plants of that associes as already described (page 337).

In making reservoirs of Gull, Leech and Winnebegoshish lakes,

the water-level has been raised several feet over extensive areas surrounding these lakes and along rivers tributary to them. In the same way the building of dams in rivers to obtain power for lighting or for the operation of machinery has resulted in the initiation of secondary successions along the rivers affected for a distance of several miles above the dams. Man has been the agent in causing these successions. Beavers, by building dams across streams, cause a flooding of areas along the streams for some distance above the dams. The areas affected by beaver dams, however, are usually small, although such areas are found quite often.

The topography of a region determines in a large measure the extent to which an area may be affected by flooding and consequently determines the stage at which secondary succession will begin. If the shore of a lake or banks of a stream are high and steep, a rise of several feet in the water-level may produce no very evident effect. On the other hand, if a lake or river is bordered by marsh or swamp, a rise of a foot or even of a few inches may affect the vegetation to a marked extent. The shores of Leech and Winnebegoshish lakes are diverse in character, but for the most part are sufficiently high and steep so that the raising of the water-level by the conversion of the lakes into reservoirs has not affected succession except in rather local areas. Leech Lake furnishes the best example of succession.

Leech Lake, on the east side, between Leech Lake River and Boy River and south about an equal distance, is bordered by a tamarack swamp. Similar swamps occur at the north end of Sucker Bay, on the west side of the same bay and at the north end of Steamboat Bay and along Steamboat River. The swamps also form a zone along streams tributary to Leech Lake at the places named.

The rise of the water-level has resulted in the killing of the tamaracks in the areas above named, except along the margins. As a result, the *Larix-Picea* associes has been replaced by a *Carex-Calamagrostis* associes, which is similar in all its characteristic features to the *Carex* associes as described under primary succession (page 340), except that *Calamagrostis canadensis* and *C. hyperborea* become codominants with the species of *Carex*.

In the deeper water bordering the zone of *Carex-Calamagrostis*, *Zizania* and *Phragmites* occur. Along with these, especially near the mouth of Boy River, *Equisetum fluviatile* appears conspicuously as a socies, often dominating quite extensive areas. *Scirpus* and

Typha were absent from nearly all of

In deeper water just outside the Z
talia-Nymphaea and *Potamogeton* w
presence or absence is to be explained
of the lake bottom.

Young trees of *Larix, Betula pumi*
and others were found as invaders alo
Carex-Calamagrostis zone of the s
pumila and *Salix candida* usually occ
the shoreward, *Larix* occurred, and w
it were found *Ledum* and *Cornus st*
and establishment of *Larix* and *Pice*
restored.

2. BURN OR CLEARING

a. IN THE CLIMA

The removal of the climax forest
the soil to a greater or lesser extent
passage of fire, and second by expos
wind, in case of either burning or cle
greatly changed also, and many of t
ground layer in the forest disappear
dure the intense light and increased t

Although initiated by distinctly d
succession is essentially or, sometime
ference being of degree and not of k
great extent and fierceness, may aff
that all the under-vegetation and ev
face of the ground may be burned an
and perennial underground parts are
must begin anew. If such a burn occ
crop, the succession may be a primar
lichens, or a secondary one beginni
lichens. Clearing alone would never
sand, clay, loam, or mixtures of these
parts and seeds would not be destro
cession to begin at a later stage.
together, as where the brush and s
valuable timber has been removed.
structive and allow succession to beg

Typha were absent from nearly all of the areas observed.

In deeper water just outside the *Zizania-Phragmites* zone, *Castalia-Nymphaea* and *Potamogeton* were sometimes found. Their presence or absence is to be explained by the topography and nature of the lake bottom.

Young trees of *Larix, Betula pumila, Salix candida, S. petiolaris* and others were found as invaders along the shoreward edge of the *Carex-Calamagrostis* zone of the secondary succession. *Betula pumila* and *Salix candida* usually occurred farthest out. More to the shoreward, *Larix* occurred, and with it or sometimes preceding it were found *Ledum* and *Cornus stolonifera.* With the invasion and establishment of *Larix* and *Picea,* the original conditions are restored.

2. BURN OR CLEARING SUCCESSION

a. IN THE CLIMAX FOREST

The removal of the climax forests affects the water-content of the soil to a greater or lesser extent by drying the soil, first by the passage of fire, and second by exposure to the action of sun and wind, in case of either burning or clearing. The light relations are greatly changed also, and many of the characteristic plants of the ground layer in the forest disappear, since they are unable to endure the intense light and increased transpiration attendant thereon.

Although initiated by distinctly different causes, the course of succession is essentially or, sometimes, precisely the same, the difference being of degree and not of kind. Fires, particularly if of great extent and fierceness, may affect an area more seriously in that all the under-vegetation and even the leaf-mould on the surface of the ground may be burned and removed completely. Seeds and perennial underground parts are thus destroyed and succession must begin anew. If such a burn occurs in a region with rock outcrop, the succession may be a primary one beginning with crustose lichens, or a secondary one beginning with foliose and fruticose lichens. Clearing alone would never bring this about. In areas of sand, clay, loam, or mixtures of these, the deeper-lying underground parts and seeds would not be destroyed and would enable the succession to begin at a later stage. These two causes often work together, as where the brush and slashings are burned after the valuable timber has been removed. Fires of such kind are less destructive and allow succession to begin at a later stage than would

otherwise happen.

Windthrows, whether affecting a considerable number of trees as a group or only a single individual, give rise to secondary successions. These are to be considered with clearing succession from which they differ in no essential respect. The fact that the clearing has been brought about by the action of a biotic agency in one case and by a natural force in another is of no significance.

The extent of the area cleared or burned affects the succession by modifying the rate of migration into the burn or clearing. This is particularly true in case of destructive fires where seeds or propagules on or near the surface are killed by the heat of the fire. Over large burned or cleared areas, invasion would be greatest near the edge because of the greater number of disseminules carried by wind from the surrounding forest. Light disseminules carried by wind could invade farther and in greater number than those with heavy seeds or fruits. *Populus* and *Betula* could invade an area more rapidly, for example, than *Pinus*.

Since most of the area covered by the pine forest has been cut over in lumbering and also since most of it has been burned over at one time or another, in some places several times, the pine forest as we find it now is largely developed by secondary succession. Thus the consideration of secondary succession due to lumbering and burning is of much importance. Except for areas in which the climax pine forest has developed through hydrarch or xerarch successions, the study of succession in other areas is wholly a study of secondary succesion.

Since fire is more destructive to the vegetation of an area and therefore causes secondary succession to begin at an earlier or lower stage, the initiation of secondary succession as a result of burning is treated first. The successive stages are taken in order, the cause of initiation at any particular stage being indicated in the discussion of that stage.

Very destructive fires may not only remove the existing vegetation of a region, but also destroy the humus that may have accumulated on the ground and with it all the seeds and propagules of every kind so that succession must begin at a very early stage. In areas of rock where only a shallow layer of humus exists, without the presence of soil, a fire may cause the initiation of a primary succession beginning with crustose lichens. The lowest stage, however, in which a secondary succession can begin is with the

Cladonia-Polytrichum associes.

(1) THE LICHEN A

When fire sweeps over a region d forest undergrowth, various species of *cilis, C. cristatella, C. fimbriata, C. pyx* pear on the partly burned stumps a branches of trees. Scattered lichens over the surface of the ground, which sions beginning with this stage, howev the ease with which herbaceous or wo

(2) THE HERBACEOUS

The usual point at which seconda fire is with the appearance of herbs a and northeastern part of the state, *Cha* nant plant. With this in greater or found species of *Aster* and *Solidago*. latter genera vie with *Chamaenerion* such as *Agrostis hiemalis, Muhlenber thophysum, Agropyron tenerum,* and *E* always present. *Agrostis* is usually th

Other species usually present with

Anaphalis margaritacea	*Lep*
Carduus altissimus	*Onc*
Lactuca sp.	*Pte*

In places where the soil is very san siderable difference from the above. succession after fire or clearing begi *spicata* is often dominant, occurring a of *Festuca ovina*. In places not occu *uva-ursi* is often found, at times sp patches. Other plants occurring with

Achillea lanulosa	*Lec*
Antennaria canadensis	*Ory*
Aster laevis	*Sol*
Lacinaria scariosa	

A third variation in sequence is f

Cladonia-Polytrichum associes.

(1) THE LICHEN ASSOCIES

When fire sweeps over a region destroying the forest and the forest undergrowth, various species of *Cladonia,* especially *C. gracilis, C. cristatella, C. fimbriata, C. pyxidata* and *C. verticillata,* appear on the partly burned stumps and half-buried trunks and branches of trees. Scattered lichens and mosses may occur also over the surface of the ground, which is otherwise bare. Successions beginning with this stage, however, are rather rare, owing to the ease with which herbaceous or woody invaders may enter.

(2) THE HERBACEOUS ASSOCIES

The usual point at which secondary succession begins after a fire is with the appearance of herbs and grasses. In the northern and northeastern part of the state, *Chamaenerion* is often the dominant plant. With this in greater or lesser abundance are to be found species of *Aster* and *Solidago.* In some places, indeed, the latter genera vie with *Chamaenerion* as to abundance. Grasses such as *Agrostis hiemalis, Muhlenbergia racemosa, Panicum xanthophysum, Agropyron tenerum,* and *Elymus canadensis* are nearly always present. *Agrostis* is usually the most abundant.

Other species usually present with the above are:

Anaphalis margaritacea	*Leptilon canadense*
Carduus altissimus	*Onagra biennis*
Lactuca sp.	*Pteris aquilina*

In places where the soil is very sandy, the succession shows considerable difference from the above. In such places the secondary succession after fire or clearing begins with grasses. *Danthonia spicata* is often dominant, occurring alone or with an intermixture of *Festuca ovina.* In places not occupied by grass, *Arctostaphylos uva-ursi* is often found, at times spreading over quite extensive patches. Other plants occurring with these are the following:

Achillea lanulosa	*Lechea stricta*
Antennaria canadensis	*Oryzopsis juncea*
Aster laevis	*Solidago nemoralis*
Lacinaria scariosa	

A third variation in sequence is found to exist. This, too, is

found in sandy soil and near the southern limit of the pine forest approaching the prairie. Here a burned or cleared area soon passes into an *Andropogon* associes with *A. furcatus* as the dominant species. *A. scoparius, Stipa spartea, Agropyron caninum* and *Poa nemoralis* are usually found with *A. furcatus,* but not very abundantly. Apparently it happens that *Danthonia* and various herbs as described above come in first, only to be replaced by *Andropogon,* which crowds out the other plants. Other secondary species occurring with *A. furcatus* are the following:

Achillea lanulosa	*Campanula rotundifolia*
Agastache anethiodora	*Equisetum hiemale*
Agrostis hiemalis	*Erigeron ramosus*
Artemisia caudata	*Helianthemum canadense*
Aster laevis	*Hieracium umbellatum*
Bromus kalmii	*Lacinaria scariosa*

When an area has been plowed after clearing and then abandoned, it grows up for a few years to ruderals and semi-ruderals, such as *Leptilon canadense, Chenopodium album, Amaranthus retroflexus, A. graecizans, Onagra biennis, Achillea lanulosa, Erigeron ramosus* and such grasses as *Agropyron tenerum, A. caninum, Elymus canadensis* and *Agrostis alba.* The grasses tend to increase and crowd out the weeds, but before the grasses gain control the area is usually invaded by shrubs and trees, which become dominant at the expense of both weeds and grasses.

(3) *Corylus-Rubus* Associes

Following fires of less intensity and following the removal of the forest by clearing, secondary succession may begin with an associes of *Rubus strigosus* and *Corylus americana.* This is more often true after clearing than after burning, since the former does not destroy any under-shrubs which may be present. In a secondary succession beginning with one of the lower stages, the shrubs invade the herbaceous associes and soon become dominant by crowding out the herbs. Usually the invasion begins with the appearance of *Diervilla lonicera* in the herbaceous associes, to be followed soon by *Corylus* and *Rubus.* In the area near Ely where the surface is largely of rock, *Comptonia peregrina, Pteris aquilina* and *Diervilla lonicera* with *Chamaenerion* and *Aster* constitute a stage prior to the appearance of the *Rubus-Corylus* associes.

Consocies: The species most often f
associes, as indicated in the name, are *Ri*
americana. Alnus crispa and *Prunus pe*
as consocies, or in places may replace
dominants. *Alnus,* however, usually re
only in areas where the water-content o

Secondary species: In many places
less abundant and must rank as a second
occurs in some areas also. In rather m
the latter, *Corylus rostrata, Salix disco*
willows occur abundantly. The usual
associes are:

Anaphalis margaritacea	*Lacin*
Aster laevis	*Onagr*
Chamaenerion angustifo-	*Pteris*
lium	*Solida*
Diervilla lonicera	*Solida*

Many other species are to be found,
which have persisted after its removal
of grass with their attendant secondary
replaced by the shrubs of this associes.

(4) *Populus-Pinus divaricat*

The presence of shrubs of the *Corylu*
keep the soil of the habitat moist and pro
ing them, and thereby enables the trees
established.

Some notable variations in this seque
cases *Pinus divaricata* and *Populus tre*
become dominant directly following the r
est without the appearance of the usual a
often found to occur in the area of sa
southern Beltrami, parts of Cass, Hubb
Crow Wing counties, particularly with
cata. It may occur also in other districts,
the water-content of the soil is not high
apt to become an early dominant in place

It has been observed, in some places,
may become the dominant after burning

Consocies: The species most often found as dominants of this associes, as indicated in the name, are *Rubus strigosus* and *Corylus americana*. *Alnus crispa* and *Prunus pennsylvanica* may be found as consocies, or in places may replace one or both of the usual dominants. *Alnus,* however, usually replaces *Corylus* and *Rubus* only in areas where the water-content of the soil is greater.

Secondary species: In many places, *Prunus pennsylvanica* is less abundant and must rank as a secondary species. *Alnus incana* occurs in some areas also. In rather moister soil and often with the latter, *Corylus rostrata, Salix discolor* and sometimes other willows occur abundantly. The usual secondary species of this associes are:

Anaphalis margaritacea	*Lacinaria scariosa*
Aster laevis	*Onagra biennis*
Chamaenerion angustifo-	*Pteris aquilina*
lium	*Solidago canadensis*
Diervilla lonicera	*Solidago nemoralis*

Many other species are to be found, viz., plants of the forest which have persisted after its removal or destruction and patches of grass with their attendant secondary species that have not been replaced by the shrubs of this associes.

(4) *Populus-Pinus divaricata* Associes.

The presence of shrubs of the *Corylus-Rubus* associes serves to keep the soil of the habitat moist and protect the seedlings by shading them, and thereby enables the trees of the associes to become established.

Some notable variations in this sequence may occur. In some cases *Pinus divaricata* and *Populus tremuloides* may invade and become dominant directly following the removal of the climax forest without the appearance of the usual antecedent stages. This is often found to occur in the area of sand and gravel outwash in southern Beltrami, parts of Cass, Hubbard, Wadena, Becker and Crow Wing counties, particularly with reference to *Pinus divaricata*. It may occur also in other districts, especially in places where the water-content of the soil is not high. *Populus tremuloides* is apt to become an early dominant in places of greater water-content.

It has been observed, in some places, that *Andropogon furcatus* may become the dominant after burning or clearing, and that *Pinus*

divaricata may invade the grass directly without a previous development of shrubs. Sometimes *P. divaricata* alone invades, at other times it may be accompanied by *Betula papyrifera* or by *Quercus coccinea* or both.

Consocies: The usual dominants are *Populus tremuloides, Pinus divaricata* and *Betula papyrifera.* To these *Quercus coccinea* may be added for certain areas. Any two or more of these may form a mixture, or in other places the associes may be represented by but one of its consocies.

In the region of surface rock, near Tower and Ely, *Betula papyrifera* often occurs as an exclusive dominant over areas of considerable extent. The same may be said of *P. divaricata* in the same area, but more particularly is this true of *P. divaricata* in the areas of outwash sand and gravel above mentioned. In Crow Wing county, *Quercus coccinea* occurs as a consocies. This has not been found to apply elsewhere. In areas of greater water-content in the soil, *P. tremuloides* may occur as an exclusive dominant.

Secondary species: Other species of *Populus,* viz.: *P. grandidentata* and *P. balsamifera,* usually occur with *P. tremuloides,* but not in sufficient abundance to rank as consocies. Colonies of *P. grandidentata* may occur sometimes. *Quercus coccinea* is present in many places.

A number of shrubs are characteristic of this associes in secondary succession:

Acer spicatum	*Prunus virginiana*
Alnus incana	*Ribes floridum*
Cornus stolonifera	*Rosa acicularis*
Corylus rostrata	*Rosa blanda*
Diervilla lonicera	*Rubus strigosus*
Lonicera oblongifolia	*Vaccinium canadense*
Prunus pennsylvanica	*Vaccinium pennsylvanicum*

In some areas *Alnus crispa* may be found with *A. incana. Lonicera hirsuta, Ribes gracile* and *Rubus procumbens* occur occasionally.

The herbs of this associes are numerous. The following are usually present:

Anemone quinquefolia	*Aster cordifolius*
Aralia nudicaulis	*Aster laevis*

Aster macrophyllus	*Lyc*
Chimaphila umbellata	*Ma*
Cornus canadensis	*Ory*
Epipactis pubescens	*Pte*
Falcata comosa	*Pyr*
Fragaria virginiana	*Pyr*
Gaultheria procumbens	*Rub*
Lathyrus venosus	*Vio*
Lycopodium clavatum	

Arctostaphylos uva-ursi and *Dan* usually in abundance, *Arctostaphylos* surface of the ground. These were fo and gravel outwash, and were not no *complanatum* occurs in the northeaste not been observed at other places. *Ep* tain areas and often is very abundant stricted to sandy soils on which pines

The following may be present, bu individuals or in restricted areas: *A Clintonia borealis, Comandra umbellat patica triloba* and *Lathyrus ochroleuc*

Pinus resinosa and *P. strobus* of to invade this associes, especially in a windthrows or to death of one or a *Pinus divaricata* and *Populus tremulo* wood of both is brittle, and the trees a so that the opportunity for invasion b climax forest is soon presented. The forest and its characteristic secondary discussed (page 345) and need not be

b. Secondary Succession in the

Although the *Larix-Picea* associes the development of the climax pine for persists indefinitely as a subclimax on ences in the habitat as compared with est. The very different habitat condi ferences in the vegetation and in a di successional stages, which makes it n

Aster macrophyllus
Chimaphila umbellata
Cornus canadensis
Epipactis pubescens
Falcata comosa
Fragaria virginiana
Gaultheria procumbens
Lathyrus venosus
Lycopodium clavatum
Lycopodium obscurum
Maianthemum canadense
Oryzopsis asperifolia
Pteris aquilina
Pyrola americana
Pyrola secunda
Rubus triflorus
Viola conspersa

Arctostaphylos uva-ursi and *Danthonia spicata* are present, usually in abundance, *Arctostaphylos* forming broad mats over the surface of the ground. These were found only in the area of sand and gravel outwash, and were not noted elsewhere. *Lycopodium complanatum* occurs in the northeastern part of the state, but has not been observed at other places. *Epigaea repens* is found in certain areas and often is very abundant locally. Apparently it is restricted to sandy soils on which pines have become dominant.

The following may be present, but usually only as scattered individuals or in restricted areas: *Apocynum androsaemifolium, Clintonia borealis, Comandra umbellata, Habenaria orbiculata, Hepatica triloba* and *Lathyrus ochroleucus.*

Pinus resinosa and *P. strobus* of the climax association begin to invade this associes, especially in any gaps that occur due to windthrows or to death of one or a few trees from any cause. *Pinus divaricata* and *Populus tremuloides* are both short-lived, the wood of both is brittle, and the trees are easily broken off by wind, so that the opportunity for invasion by the long-lived pines of the climax forest is soon presented. The composition of the climax forest and its characteristic secondary species have already been discussed (page 345) and need not be repeated here.

b. Secondary Succession in the *Larix-Picea* Subclimax

Although the *Larix-Picea* associes represents only a stage in the development of the climax pine forest, it is a stage which often persists indefinitely as a subclimax on account of the great differences in the habitat as compared with that of the climax pine forest. The very different habitat conditions result in marked differences in the vegetation and in a difference in the sequence of successional stages, which makes it necessary to treat secondary

succession in tamarack swamps under a special heading.

The causes work in the same way and may operate singly or together, as indicated elsewhere. Fire as the more destructive agent affects the habitat more profoundly and causes succession to begin at a lower stage. This is especially true if burning occurs during a dry season when the *Sphagnum* surface is partly dry. At such times burning may result in killing out the *Sphagnum* and in the initiation of a secondary succession beginning with *Carex-Calamagrostis*. The sequence of stages after the appearance of *Carex-Calamagrostis* up to *Larix-Picea* is essentially that of primary succession. In some instances *Populus* may invade directly after a fire so that a dense growth of seedling poplars is the dominant vegetation.

When a tamarack swamp is drained and afterwards burned, the succession begins usually with the *Carex-Calamagrostis* associes. As a result of the combined draining and burning, all the characteristic plants of the swamp disappear. The water-content of the habitat is still high but much less than if *Sphagnum* were present. The disappearance of *Sphagnum, Larix* and other swamp species permits the invasion of *Carex* and *Calamagrostis,* so that the *Larix-Picea* stage comes to be replaced by the associes of *Carex-Calamagrostis* as the first stage of secondary succession initiated by draining and burning. If the area affected be mowed or burned over each year, it may be kept indefinitely in this stage and valuable hay meadows result. If the swamp be kept drained but not mowed or burned over, a secondary succession culminating in the climax pine forest will ultimately result.

In such a case the *Carex-Calamagrostis* associes is invaded first by *Betula pumila, Salix petiolaris,* soon followed by *Salix bebbii, S. discolor, Cornus stolonifera* and *Alnus incana.* As a result of the invasion of these, the plants of the *Carex-Calamagrostis* associes are killed out. The swamp gradually fills up by the washing-in of soil around the edge, aided by the accumulation of humus from the decay of dead vegetation. The process of filling reduces the water-content of the soil and permits the invasion of *Populus, Abies, Betula* and sometimes *Fraxinus nigra.* The invasion proceeds from the edge, gradually encroaching on the swamp. After a time the associes of *Abies-Betula* as described on page 344 becomes established. This is later invaded by pines as already described in normal primary succession. The successional stages of

secondary succession in drained swam
to the climax pines appear more rapi
succession, but in stages common to bo
mon associes and the secondary specie
essentially alike.

The removal of the dominant *Lari*
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In extensive swamp areas where f
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velop, and with the appearance of ne
original *Larix-Picea* associes soon bec

In small swamps and in a zone alo
where the soil is built up more as the
of *Alnus incana, Cornus stolonifera*
after the removal of *Larix* and *Picea*
oblongifolia, Ribes hudsonianum and
abundantly with these.

Windthrows are to be regarded a
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at once by *Larix* and *Picea* or by eit
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deep swamps where *Sphagnum* is abu

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Betula and *Populus* appear in the plac
Alnus incana, Salix discolor and *Cor*
also, but these are later replaced by th
swamp fills up, an *Abies-Betula* assoc
succeeded finally by the climax pine f
is carried still further.

secondary succession in drained swamps from the initial stage up to the climax pines appear more rapidly than in normal primary succession, but in stages common to both the composition of a common associes and the secondary species present in that associes are essentially alike.

The removal of the dominant *Larix-Picea* layer without subsequent burning does not seriously affect the successional sequence since the water relations of the habitat remain essentially unchanged. The most marked effects are in the changed light relations and increased exposure to evaporation. These changes may result in the disappearance of some of the shade-loving plants.

In extensive swamp areas where filling from the edge can not alter the general conditions of the swamp, the effect of clearing is to permit the development of the bog shrubs which had been suppressed by the tamarack and spruce and consequently in the reestablishment of an associes of *Ledum, Andromeda* and *Chamaedaphne*. Usually the clearing is not complete, a greater or lesser number of young tamarack and spruce being left. These now develop, and with the appearance of new tamarack and spruce, the original *Larix-Picea* associes soon becomes dominant again.

In small swamps and in a zone along the edge of larger swamps where the soil is built up more as the result of filling-in, an associes of *Alnus incana, Cornus stolonifera* and species of *Salix* appears after the removal of *Larix* and *Picea*. *Betula pumila, Lonicera oblongifolia, Ribes hudsonianum* and *R. triste* occur more or less abundantly with these.

Windthrows are to be regarded as miniature clearings. In a *Larix-Picea* swamp, when a windthrow occurs, its place is invaded at once by *Larix* and *Picea* or by either of these alone, which results in keeping the area indefinitely in the same developmental stage in spite of the prevalence of windthrows. This applies in deep swamps where *Sphagnum* is abundantly developed.

In swamps that are more nearly filled up and where in consequence *Sphagnum* makes little or no growth, *Picea, Thuja, Abies, Betula* and *Populus* appear in the places left vacant by windthrows. *Alnus incana, Salix discolor* and *Cornus stolonifera* often come in also, but these are later replaced by the trees named above. As the swamp fills up, an *Abies-Betula* associes becomes established to be succeeded finally by the climax pine forest as the process of filling is carried still further.

A *Larix-Picea* swamp, if drained and not disturbed by clearing or burning, gradually fills up, thereby reducing the water-content of the soil. With the draining away of the water and the filling-up, *Sphagnum* disappears. As the filling-up proceeds, *Larix* dies out, *Picea* and *Thuja* taking its place. In time *Abies balsamea, Betula papyrifera* and *Fraxinus nigra* come in also, the invasion proceeding from the edge where filling occurs most rapidly. As a result of drainage not complicated by the introduction of other factors, the normal primary succession occurs from *Larix-Picea* through the *Abies-Betula* associes to the climax pine. Thus it appears that drainage alone merely accelerates the normal primary succession.

ACER-TILIA ASSOCIATION

I. Primary Succession

1. HYDRARCH SUCCESSION

Initial causes: The formation of bodies of water of sufficient size and depth to completely denude affected areas provides conditions for the initiation of primary succession. The origin of lakes in Minnesota has been indicated briefly under "Initial Causes" in the discussion of primary succession in the area of the pine forest climax.

A succession having its origin in water and culminating in the *Acer-Tilia* climax association shows a series of stages as follows:

(1) *Chara-Philotria* Associes
(2) *Castalia-Nymphaea* Associes
(3) *Scirpus-Zizania* Associes
(4) *Carex* Associes
(5) *Larix-Picea* Associes
(6) *Populus-Betula* Associes
(7) *Acer-Tilia* Association

A variation of this sequence may occur by the failure of the *Larix-Picea* associes to develop between the *Carex* associes and the climax association. This is true particularly where the land rises rather abruptly from a swamp or meadow, resulting in a sudden drop in the water-content of the soil. In some instances the *Larix-Picea* associes is found to be preceded by a *Chamaedaphne-Andromeda* associes, while in other instances the latter does not appear. Which of these variations is to be regarded as the rule and which the exception it is not possible to state from evidence now available. When more places in the deciduous belt have been studied a

definite answer can be made with refe

Since the stages in the development max in many respects are the same as the development of the pine forest c stricted to the pointing out of differen

(1) *Chara-Philotria*

As to causes, consocies and second here is the same as the initial stage le climax which is discussed on page 33

(2) *Castalia-Nymphae*

This associes is similar to the corre velopment of the pine forest climax t (See discussion on page 337.)

(3) *Scirpus-Zizania*

See discussion of corresponding a which this shows no essential variation associes as found in Star and Dead la the very extensive area of *Zizania* whi the long shallow arms of these lakes. pearance of meadows of *Zizania*, thou one could go anywhere through it. Sh action or to the action of wind-driven the spring are free of *Zizania* and usu and others of this associes.

(4) *Carex* Ass

Causes: The filling-up of lakes or eroded material from the sides and by plant remains results in the reduction shore. This permits the invasion of p

Consocies: The following are typi cies:

Carex aquatilis — *Care*
Carex diandra — *Care*
Carex filiformis

Carex aquatilis and *C. trichocarpa* the corresponding associes of hydrarch

definite answer can be made with reference to this point.

Since the stages in the development of the deciduous forest climax in many respects are the same as the corresponding stages in the development of the pine forest climax, the discussion is restricted to the pointing out of differences, when such exist.

(1) *Chara-Philotria* Associes

As to causes, consocies and secondary species the initial stage here is the same as the initial stage leading up to the pine forest climax which is discussed on page 337.

(2) *Castalia-Nymphaea* Associes

This associes is similar to the corresponding associes in the development of the pine forest climax through hydrarch succession. (See discussion on page 337.)

(3) *Scirpus-Zizania* Associes

See discussion of corresponding associes on page 338, from which this shows no essential variation. A striking feature of this associes as found in Star and Dead lakes in Otter Tail county is the very extensive area of *Zizania* which completely filled some of the long shallow arms of these lakes. From shore it had the appearance of meadows of *Zizania,* though with a rowboat or canoe one could go anywhere through it. Shores exposed to severe wave-action or to the action of wind-driven ice as the ice breaks up in the spring are free of *Zizania* and usually also of *Scirpus, Typha* and others of this associes.

(4) *Carex* Associes

Causes: The filling-up of lakes or ponds by the washing-in of eroded material from the sides and by the accumulation of decayed plant remains results in the reduction of the water-level along the shore. This permits the invasion of plants of this associes.

Consocies: The following are typical dominants of this associes:

Carex aquatilis
Carex diandra
Carex filiformis
Carex lanuginosa
Carex trichocarpa

Carex aquatilis and *C. trichocarpa* are less prominent than in the corresponding associes of hydrarch succession culminating in

the climax pine forest, their place being taken usually by *C. filiformis, C. lanuginosa* and *diandra*. In many places the associes occupies only a narrow zone while in others it is more extensive. As in the development of the *Pinus* association so here the *Carex* associes may follow directly after the *Castalia-Nymphaea* stage with only a sparse growth of *Zizania* or *Zizania* and *Scirpus* intervening, or these may be entirely absent.

Secondary species: The following species of herbs are characteristic:

Alsine longifolia	*Lycopus lucidus*
Aster paniculatus	*Mentha canadensis*
Campanula aparinoides	*Menyanthes trifoliata*
Comarum palustre	*Naumburgia thyrsiflora*
Dryopteris thelypteris	*Scutellaria galericulata*
Galium trifidum	*Sium cicutaefolium*

(5) *Larix-Picea* Associes

Causes: The appearance of *Sphagnum* as described on pages 341 and 342 may lead up to this associes, following the *Chamaedaphne-Andromeda* associes as in the development of the climax pine forest. This has been observed in some places, but in others *Larix* may appear without being preceded by the *Chamaedaphne-Andromeda* associes. That this procedure is not to be regarded as normal but rather as a departure from it due to draining, burning, clearing or other disturbance initiating a secondary succession, seems probable. When more evidence becomes available by the study of development in other places in the deciduous forest region, this point will be decided.

Consocies: The associes consists typically of two dominants, *Larix laricina* and *Picea mariana*.

Larix ranges much farther southward than *Picea*, so that the former is often the only representative of the associes.

Secondary species: The following shrubs usually occur in this associes:

Betula pumila	*Salix cordata*
Cornus stolonifera	*Salix discolor*
Salix bebbii	*Salix petiolaris*
Salix candida	

Betula pumila and *Salix candida* are often the first to invade the

Carex associes and sometimes form
and the *Larix* zone. The herbs of th
the *Carex* stage with its characterist
usually persist as relicts in the *Larix-*

(6) *Populus-Betula*

Causes: Further filling along th
washing-in of eroded material and by
matter from decay of plant bodies r
water-content. The development of
sults in the more or less complete di
sedges, or in their reduction. Where
or in vacant places resulting from win
are able to invade and in time become

Consocies: The species usually
Betula papyrifera, Populus tremuloid
balsamifera. Fraxinus nigra is often
sufficient numbers to rank as a conso
grandidentata are usually the most a
not appear at all, the associes being
Betula.

Secondary species: The undergr
ing shrubs:

Cornus stolonifera	*Rib*
Corylus americana	*Ro*
Parthenocissus quinquefolia	*Ru*

The following are the most abunda

Aralia nudicaulis	*Ga*
Aster macrophyllus	*Ma*
Carex longirostris	*Or*
Circaea alpina	*Ph*
Circaea lutetiana	*Py*
Cystopteris fragilis	*Ra*
Dryopteris cristata	*Ru*
Erigeron philadelphicus	*Sm*
Festuca nutans	*Vi*
Fragaria americana	*Vi*

Carex associes and sometimes form a scattering zone between it and the *Larix* zone. The herbs of this stage are the consocies of the *Carex* stage with its characteristic secondary species, which usually persist as relicts in the *Larix-Picea* associes.

(6) *Populus-Betula* Associes

Causes: Further filling along the edge of swamps by the washing-in of eroded material and by the accumulation of organic matter from decay of plant bodies results in a reduction in the water-content. The development of the *Larix-Picea* associes results in the more or less complete disappearance of grasses and sedges, or in their reduction. Where the tamaracks are dying out, or in vacant places resulting from windthrows, *Populus* and *Betula* are able to invade and in time become established.

Consocies: The species usually appearing as dominants are: *Betula papyrifera, Populus tremuloides, P. grandidentata,* and *P. balsamifera. Fraxinus nigra* is often found with these but not in sufficient numbers to rank as a consocies. *P. tremuloides* and *P. grandidentata* are usually the most abundant, but in places may not appear at all, the associes being represented in such places by *Betula.*

Secondary species: The undergrowth consists of the following shrubs:

Cornus stolonifera	*Ribes floridum*
Corylus americana	*Rosa blanda*
Parthenocissus quinquefolia	*Rubus strigosus*

The following are the most abundant plants of the ground layer:

Aralia nudicaulis	*Galium triflorum*
Aster macrophyllus	*Maianthemum canadense*
Carex longirostris	*Oryzopsis asperifolia*
Circaea alpina	*Phryma leptostachya*
Circaea lutetiana	*Pyrola americana*
Cystopteris fragilis	*Ranunculus abortivus*
Dryopteris cristata	*Rubus triflorus*
Erigeron philadelphicus	*Smilacina stellata*
Festuca nutans	*Viola conspersa*
Fragaria americana	*Viola papilionacea*

(7) *Acer-Tilia* Association

Causes: The further filling of the low area by the washing-in of soil and by the accumulation of decayed plant-remains brings about a reduction in the water-content of the soil. The habitat has now become mesophytic in character. The invasion of the *Populus-Betula* associes by the species of the climax forest occurs when the poplars or birches die out as the result of competition or when windthrows occur. The fact that *Acer, Tilia* and others of this associes are longer-lived than *Populus* and *Betula* enables them to crowd out the latter in competition.

Consocies: The dominants of this association are *Acer saccharum* and *Tilia americana*. Preceding them somewhat the following trees are dominant and constitute a subclimax:

Carya cordiformis	*Quercus alba*
Fraxinus lanceolata	*Quercus rubra*
Juglans cinerea	*Ulmus americana*

These are usually well mixed, and the exclusive dominance of any one of them is rather exceptional, although in the mature association *Acer* and *Tilia* are present in far greater numbers than any other of the usual species. In very sandy soil and further northward, *Acer* disappears and species of *Quercus* become more abundant. The presence of a large proportion of *Quercus* however, indicates just the beginning of the climax association.

Secondary species: In the upper or dominant layer may be found with the consocies occasional trees of *Betula papyrifera, B. lutea, Populus deltoides, P. balsamifera, Quercus macrocarpa,* and *Ulmus fulva*. Some of these, such as *Betula* and *Populus,* have persisted from the preceding associes.

The usual small trees and shrubs of this associes are:

Acer spicatum	*Parthenocissus quinquefolia*
Amelanchier canadensis	*Prunus americana*
Amelanchier oblongifolia	*Prunus virginiana*
Cornus stolonifera	*Rhus rydbergii*
Corylus americana	*Ribes floridum*
Crataegus macracantha	*Ribes cynosbati*
Crataegus punctata	*Ribes gracile*
Crataegus rotundifolia	*Rosa blanda*
Ostrya virginiana	

Rubus strigosus
Symphoricarpos occidentalis
Viburnum opulus

Forming thickets along the edge o
cana, P. virginiana, Rhus glabra, R. hi
nus stolonifera, C. paniculata, Ribes
strigosus and *Symphoricarpos occiden*
nus, Rhus and *Corylus* usually form
others usually occur in mixtures and
nies. In some places all of these may
ously. *Ceanothus ovatus* occurs abunc

The following are the characteristi
in the *Acer-Tilia* climax forest:

Actaea rubra	*Lo*
Adiantum pedatum	*Ma*
Anemone quinquefolia	*Ph*
Aquilegia canadensis	*Pol*
Aralia nudicaulis	*Ru*
Arisaema triphyllum	*Sa*
Aster cordifolius	*Sa*
Aster macrophyllus	*Sm*
Bicuculla cucullaria	*Sm*
Carex laxiflora	*Sm*
Carex longirostris	*Sy*
Erigeron philadelphicus	*Th*
Fragaria americana	*Th*
Fragaria virginiana	*Tri*
Galium aparine	*Ur*
Galium triflorum	*Uv*
Hepatica acuta	*Vi*
Hepatica triloba	*Vi*
Hydrophyllum virginianum	*Vi*

The following may be found occas

Aralia racemosa	*Or*
Caulophyllum thalictroides	*Os*
Dryopteris cristata	*Os*
Meibomia grandiflora	*Os*
Oakesia sessiliflora	*Pol*
Onoclea sensibilis	

Rubus strigosus
Symphoricarpos occidentalis
Viburnum opulus
Vitis vulpina
Xanthoxylum americanum

Forming thickets along the edge of the woods, *Prunus americana, P. virginiana, Rhus glabra, R. hirta, Corylus americana, Cornus stolonifera, C. paniculata, Ribes gracile, Rosa blanda, Rubus strigosus* and *Symphoricarpos occidentalis* occur commonly. *Prunus, Rhus* and *Corylus* usually form families or colonies. The others usually occur in mixtures and rarely form families or colonies. In some places all of these may be scattered quite promiscuously. *Ceanothus ovatus* occurs abundantly in a few localities.

The following are the characteristic plants of the ground layer in the *Acer-Tilia* climax forest:

Actaea rubra
Adiantum pedatum
Anemone quinquefolia
Aquilegia canadensis
Aralia nudicaulis
Arisaema triphyllum
Aster cordifolius
Aster macrophyllus
Bicuculla cucullaria
Carex laxiflora
Carex longirostris
Erigeron philadelphicus
Fragaria americana
Fragaria virginiana
Galium aparine
Galium triflorum
Hepatica acuta
Hepatica triloba
Hydrophyllum virginianum
Lonicera dioica
Maianthemum canadense
Phlox divaricata
Polygonatum commutatum
Rubus triflorus
Sanguinaria canadensis
Sanicula marilandica
Smilacina racemosa
Smilacina stellata
Smilax herbacea
Syndesmon thalictroides
Thalictrum dasycarpum
Thalictrum dioecum
Trillium cernuum
Urticastrum divaricatum
Uvularia grandiflora
Viola papilionacea
Viola pubescens
Viola sororia

The following may be found occasionally:

Aralia racemosa
Caulophyllum thalictroides
Dryopteris cristata
Meibomia grandiflora
Oakesia sessiliflora
Onoclea sensibilis
Orchis spectabilis
Osmunda cinnamomea
Osmunda claytoniana
Osmunda regalis
Polygonatum biflorum

In low places, *Urtica gracilis, Urticastrum divaricatum* and *Matteuccia struthiopteris* may occur in dense colonies or only as scattered individuals.

II. Secondary Succession

Secondary succession in the climax deciduous forest region as in the pine forest climax is of two kinds, namely:

1. Flood succession
2. Burn or clearing succession

1. FLOOD SUCCESSION

The survey party has made no specific study of secondary succession resulting from flooding by lakes or streams in any of the deciduous areas. The general course of development may be indicated, however, leaving the discussion of details for a later report. Flood successions occur most frequently along river valleys and are due to silting-up of rivers, which ponds the water above the place where silting occurs, or to the formation of small lakes on the flood plain of a river during a period of overflow. Usually the water is sufficiently shallow so that the succession can begin with the appearance of *Typha, Scirpus* and *Phragmites. Phragmites* and *Spartina* grow in very shallow water or in mud, so that they are usually most abundant along the margin of lakes where the water-level fluctuates, or on flood plains. These are followed by species of *Carex* of which *C. trichocarpa* is probably most abundant. With it are usually to be found *Calamagrostis, Panicularia americana* and *Spartina.* As filling of the flooded area proceeds, species of *Salix* and *Populus* are able to invade and still later *Acer negundo,* and finally the subclimax dominants *Ulmus* and *Fraxinus,* followed by *Tilia* and *Acer saccharum.* If flooding is recurrent the succession may be held in the *Typha-Phragmites* stage, or if the depth of water is less, in the *Carex-Calamagrostis* stage.

2. BURN OR CLEARING SUCCESSION

a. In the Climax Forest

Causes: The removal of the climax forest by burning or clearing is the fundamental cause of the initiation of secondary succession. Either of these causes results in a drier habitat, since the soil is directly exposed to the drying action of sun and wind. Plants

growing in such areas are likewise expo
sun and wind, and in consequence only
ally adapted to prevent or check tra
capable of physiological adjustment to
grow in the altered environment. The
it affects the plants by modifying tran
the evaporation of water from the soi
ation.

The secondary succession which f
deciduous forests consists of the follow

(1) *Andropogon-Stipa* Associes
(2) *Corylus-Rubus* Associes
(3) *Populus-Betula* Associes
(4) *Acer-Tilia* Association

(1) *Andropogon-Stipa*

Fires in deciduous forests rarely ga
However, where a deciduous forest jo
which is burned occasionally or annual
the edge of the forest, and in time th
placed by the prairie, which can maintai

Consocies: In parts of Meeker, Otte
ties, small areas of prairie often join
In such areas *Andropogon furcatus* an
socies. *Andropogon* is generally much
the latter occurring as families or colon

Secondary species: Other grasses
parius, Agropyrum caninum, Agrostis h
are to be found usually with the cons
are characteristic: *Campanula rotu*
Phlox pilosa, Heuchera hispida, Peta
nemoralis and *S. missouriensis.*

When clearings are cultivated for
succession differs from that just desc
all the under-shrubs and the succession
This stage is an herbaceous associes o
Abandoned fields are soon covered wi
are more or less abundant in poorly c
ceous associes of the deciduous area in
coniferous area (see page 349). Hov

growing in such areas are likewise exposed to the drying action of sun and wind, and in consequence only those which are structurally adapted to prevent or check transportation, or which are capable of physiological adjustment to such conditions, are able to grow in the altered environment. The changed light relation, since it affects the plants by modifying transpiration and by increasing the evaporation of water from the soil, is an important consideration.

The secondary succession which follows clearings of upland deciduous forests consists of the following stages:

(1) *Andropogon-Stipa* Associes
(2) *Corylus-Rubus* Associes
(3) *Populus-Betula* Associes
(4) *Acer-Tilia* Association

(1) *Andropogon-Stipa* Associes

Fires in deciduous forests rarely gain headway as under pines. However, where a deciduous forest joins a prairie or a meadow which is burned occasionally or annually, the fire tends to destroy the edge of the forest, and in time the climax forest may be replaced by the prairie, which can maintain itself if burning continues.

Consocies: In parts of Meeker, Otter Tail and Crow Wing counties, small areas of prairie often join tracts of the climax forest. In such areas *Andropogon furcatus* and *Stipa spartea* are the consocies. *Andropogon* is generally much more abundant than *Stipa*, the latter occurring as families or colonies in the *Andropogon* areas.

Secondary species: Other grasses such as *Andropogon scoparius, Agropyrum caninum, Agrostis hiemalis* and *Koeleria cristata* are to be found usually with the consocies. The following herbs are characteristic: *Campanula rotundifolia, Achillea lanulosa, Phlox pilosa, Heuchera hispida, Petalostemon candidus, Solidago nemoralis* and *S. missouriensis.*

When clearings are cultivated for a time and abandoned, the succession differs from that just described. Cultivation destroys all the under-shrubs and the succession must begin at a lower stage. This stage is an herbaceous associes of the uncultivated clearings. Abandoned fields are soon covered with weeds and grasses which are more or less abundant in poorly cultivated fields. The herbaceous associes of the deciduous area in main is similar to that of the coniferous area (see page 349). However, where the deciduous

clearing is near the prairie more of the prairie species invade.

(2) *Corylus-Rubus* Associes

The *Andropogon-Stipa* associes will be maintained as long as the fires recur with sufficient frequency to kill out any invading shrubs or trees, as for example when an area is burned annually. Prairie that has developed as the result of repeated burning of an area may be invaded by *Corylus, Rubus, Rhus* and *Rosa*. This occurs always when a prairie area near woodland ceases to be burned repeatedly, so that the shrubs become established. The covering of grasses and herbs protects the seedlings of the shrubs which soon grow up. As these increase in number by the appearance of other seedlings and by sprouts from older plants, the grasses are killed out and the typical shrub associes takes its place. Clearing alone usually results in the initiation of a secondary succession beginning with this stage. When the forest is removed and the land left uncultivated, the shrubs which have been suppressed because of shade can now develop. *Corylus* soon becomes the dominant shrub. *Rubus,* if not present in the climax forest, is one of the earliest invaders.

Consocies: *Corylus americana* and *Rubus strigosus* are the usual dominants. *Rhus hirta* and *R. glabra* often occur as socies in this associes.

Secondary species: The most abundant secondary shrubs are *Rosa blanda, R. arkansana, Symphoricarpos occidentalis, Ribes gracile* and *Rhus rydbergii.*

Herbs common to this associes will depend on many conditions, as the character of the surface soil, the plants present in the surrounding region, the time of clearing and the rapidity with which *Corylus* makes a covering. The following may be carried over from the climax association and persist under the *Corylus* if it is not too dry from the time of clearing until shade is re-established:

Actaea rubra
Aralia nudicaulis
Erigeron philadelphicus
Fragaria virginiana
Lathyrus ochroleucus
Lathyrus venosus
Maianthemum canadanse
Polygonatum commutatum
Sanicula marilandica
Smilacina stellata
Uvularia grandiflora
Vicia americana
Viola papilionacea
Viola sororia
Washingtonia longistylis

Those present as a result of invasion
canadensis, Onagra biennis, Solidago c
such grasses as *Elymus canadensis, E.*
num, A. tenerum and *Agrostis alba.*

When the climax forest is removed
a time and then abandoned, the shrub a
than in the succession of uncultivated
does not exist long before *Populus, Bet*
ter, and the succession passes rapidly f
the *Populus-Betula* associes. The chief
are: *Rubus strigosus, Rhus glabra, R.*
Symphoricarpos occidentalis. The her
licts of the preceding associes. After
its accompanying species has invaded, t
then to the climax is essentially the sam
vated clearing on pages 359 to 361.

(3) *Populus-Betula* A

The presence of shrubs of the *Cory*
tecting the soil from exposure to the
higher water-content in the soil. The sl
to seedlings of *Populus* and *Betula* fr
thereby permitting them to become estal

Consocies: The consocies of this sta
P. grandidentata and *Betula papyrifer*
soon appear after the establishment of
spaces not occupied by the latter. Th
Corylus, and several years are sometim
rise above the tops of *Corylus. Populu*
clearings. The occurrence of *Betula pa*
ular. In some localities it is absent, whi
its range it is a very prominent consoc
Salix, especially *S. discolor,* are numero
Populus-Betula associes. The most im
lows:

Amelanchier canadensis
Amelanchier spicata
Cornus paniculata
Prunus serotina
Prunus virginiana
Rhus
Rosa
Samb
Xanth

Those present as a result of invasion are *Aster laevis, Erigeron canadensis, Onagra biennis, Solidago canadensis, Zizia aurea,* and such grasses as *Elymus canadensis, E. virginicus, Agropyron caninum, A. tenerum* and *Agrostis alba.*

When the climax forest is removed and the land cultivated for a time and then abandoned, the shrub associes is slower in forming than in the succession of uncultivated clearings. Furthermore it does not exist long before *Populus, Betula* and *Salix* seedlings enter, and the succession passes rapidly from the shrub associes to the *Populus-Betula* associes. The chief shrubs found in this stage are: *Rubus strigosus, Rhus glabra, R. rydbergii, Rosa blanda* and *Symphoricarpos occidentalis.* The herbs present are largely relicts of the preceding associes. After *Populus tremuloides* with its accompanying species has invaded, the succession of trees from then to the climax is essentially the same as described for uncultivated clearing on pages 359 to 361.

(3) *Populus-Betula* Associes

The presence of shrubs of the *Corylus-Rubus* associes by protecting the soil from exposure to the sun and wind maintains a higher water-content in the soil. The shrubs also afford protection to seedlings of *Populus* and *Betula* from excessive transpiration, thereby permitting them to become established.

Consocies: The consocies of this stage are *Populus tremuloides, P. grandidentata* and *Betula papyrifera. Populus* seedlings very soon appear after the establishment of *Corylus* and *Rubus* in the spaces not occupied by the latter. Their growth is slower than *Corylus,* and several years are sometimes required for *Populus* to rise above the tops of *Corylus. Populus* appears in practically all clearings. The occurrence of *Betula papyrifera* is somewhat irregular. In some localities it is absent, while in others it is sparse. In its range it is a very prominent consocies. Sometimes species of *Salix,* especially *S. discolor,* are numerous in the early stage of the *Populus-Betula associes.* The most important shrubs are as follows:

Amelanchier canadensis
Amelanchier spicata
Cornus paniculata
Prunus serotina
Prunus virginiana
Rhus hirta
Rosa blanda
Sambucus racemosa
Xanthoxylum americanum

Occasionally *Celastrus scandens, Parthenocissus quinquefolia* and *Vitis vulpina* are found.

The herbs common to this associes are:

Actaea rubra	*Smilacina racemosa*
Anemone quinquefolia	*Smilacina stellata*
Aralia nudicaulis	*Thalictrum dioecum*
Aster drummondii	*Uvularia grandiflora*
Caulophyllum thalictroides	*Vicia americana*
Fragaria virginiana	*Viola papilionacea*
Hydrophyllum virginianum	*Viola pubescens*
Lathyrus ochroleucus	*Viola rugulosa*
Lathyrus venosus	*Viola sororia*
Sanguinaria canadensis	*Washingtonia longistylis*
Sanicula marilandica	

(4) *Acer-Tilia* Association

In the later stages of the *Populus-Betula* associes, *Fraxinus lanceolata, F. americana, Carya cordiformis, Carya ovata, Juglans cinerea, Ostrya virginiana, Quercus coccinea, Q. macrocarpa, Q. rubra, Ulmus americana* and *U. fulva* enter the associes and replace the existing dominants. This is merely a transitional stage between the *Populus-Betula* associes and the final deciduous climax stage described under the *Acer-Tilia* association on page 367. In addition to the trees mentioned above, *Acer spicatum* in the northern and eastern edge of the deciduous climax association enters in the final stages of the *Populus-Betula* associes.

b. Secondary Succession in the *Larix-Picea* Subclimax

The discussion of secondary succession in the *Larix-Picea* subclimax as given for the same subclimax in the pine forest region on page 361, applies here with but few differences. Farther south, *Picea* disappears, so that the *Larix-Picea* associes is represented by *Larix* only.

The causes work in the same way and may operate singly or together, as indicated on pages 355 and 356. Fire, as the more destructive agent, affects the habitat more profoundly and causes succession to begin at a lower stage. This is especially true if burning occurs during a dry season when the *Sphagnum* surface is partly dry. At such times burning may result in killing out the *Sphagnum* and in the initiation of a secondary succession beginning

with *Carex-Calamagrostis*. The seque
pearance of *Carex-Calamagrostis* up t
that of primary succession as indicate

When a tamarack swamp is drained
succession begins usually with the *Ca*
As a result of the combined draining
teristic plants of the swamp disappear.
habitat is still high but much less than
The disappearance of *Sphagnum, Lari*
permits the invasion of species of *Carex*
the *Larix-Picea* stage comes to be repl
first stage of secondary succession init
ing. If the area affected be mowed o
may be kept indefinitely in this stage
result. If the swamp be kept drained
over, a secondary succession culminati
forest will ultimately result.

In such a case the *Carex-Calamagr*
by *Betula pumila* and *Salix petiolaris,*
bii, S. discolor* and *Cornus stolonifer*
on the climax pine forest, *Alnus incan*
sult of the invasion of these, the plants
associes are killed out. The swamp gr
ing-in of soil around the edge, aided by
from the decay of dead vegetation. T
the water-content of the soil and perm
and *Betula,* and occasionally plants of
balsamea. Nearer the pine forest reg
abundantly. The invasion proceeds fr
croaching on the swamp. After a time
Betula, as described on page 373, bec
occurrence of a windthrow or by the d
lus or *Betula,* the spaces left vacant a
Ulmus or by two or more of them toge
are able to grow in rather dense shad
finally overtop the poplars and birches,
latter. In this way the climax *Acer-T*
page 367 under normal primary succe
The successional stages of secondary su
from the initial stage up to the climax

with *Carex-Calamagrostis*. The sequence of stages after the appearance of *Carex-Calamagrostis* up to *Larix-Picea* is essentially that of primary succession as indicated on page 364.

When a tamarack swamp is drained and afterward burned, the succession begins usually with the *Carex-Calamagrostis* associes. As a result of the combined draining and burning, all the characteristic plants of the swamp disappear. The water-content of the habitat is still high but much less than if *Sphagnum* were present. The disappearance of *Sphagnum, Larix* and other swamp species permits the invasion of species of *Carex* and *Calamagrostis,* so that the *Larix-Picea* stage comes to be replaced by this associes as the first stage of secondary succession initiated by draining and burning. If the area affected be mowed or burned over each year, it may be kept indefinitely in this stage and valuable hay meadows result. If the swamp be kept drained but not mowed nor burned over, a secondary succession culminating in the climax *Acer-Tilia* forest will ultimately result.

In such a case the *Carex-Calamagrostis* associes is invaded first by *Betula pumila* and *Salix petiolaris,* soon followed by *Salix bebbii, S. discolor* and *Cornus stolonifera.* In the region bordering on the climax pine forest, *Alnus incana* may also occur. As a result of the invasion of these, the plants of the *Carex-Calamagrostis* associes are killed out. The swamp gradually fills up by the washing-in of soil around the edge, aided by the accumulation of humus from the decay of dead vegetation. The process of filling reduces the water-content of the soil and permits the invasion of *Populus* and *Betula,* and occasionally plants of *Fraxinus nigra* and *Abies balsamea.* Nearer the pine forest region, *Abies* is present more abundantly. The invasion proceeds from the edge, gradually encroaching on the swamp. After a time an associes of *Populus* and *Betula,* as described on page 373, becomes established. With the occurrence of a windthrow or by the death of individuals of *Populus* or *Betula,* the spaces left vacant are invaded by *Acer, Tilia* or *Ulmus* or by two or more of them together. The seedlings of these are able to grow in rather dense shade, and continue until they finally overtop the poplars and birches, resulting in the death of the latter. In this way the climax *Acer-Tilia* forest, as described on page 367 under normal primary succession, becomes established. The successional stages of secondary succession in drained swamps from the initial stage up to the climax *Acer-Tilia* forest proceed

more rapidly than in normal primary succession, but in stages common to both, the composition of the associes and the secondary species present are essentially alike.

The removal of the dominant *Larix* or *Larix-Picea* layer when not followed by burning, does not seriously affect the successional sequence since the water relations of the habitat remain essentially unchanged. The most marked effects are in the changed light relations and in increased exposure to evaporation. These changes may result on the disappearance of some of the shade-loving plants.

In extensive swamp areas where filling from the edge cannot alter the general conditions of the swamp, the effect of clearing is to permit the development of the bog shrubs which had been suppressed by the tamarack and spruce, and the consequent re-establishment of an associes of *Andromeda* and *Chamaedaphne* when these are present. If *Andromeda* and *Chamaedaphne* be lacking, as happens in some areas, or present only in small numbers, an associes consisting of *Betula pumila* and species of *Salix* makes its appearance. Usually the clearing is not complete, a greater or lesser number of young tamaracks being left. These now develop and with their appearance the original dominant layer of *Larix* soon becomes established again.

In small, shallow swamps and in a zone along the edge of larger swamps where the soil is built up more as the result of filling-in, an associes of *Cornus stolonifera* and species of *Salix* appears after the removal of *Larix* and *Picea*. Farther northward, *Alnus incana* appears as one of the consocies along with *Cornus* and *Salix*. *Betula pumila* often occurs with these also.

This *Cornus-Salix* zone is later invaded by *Populus* and *Betula papyrifera*, with occasional individuals of *Abies* and *Fraxinus nigra*. The invasion of these results later in the establishment of the *Populus-Betula* associes. With the occurrence of windthrows or the death of individuals in this associes, the spaces occupied by them are invaded by seedlings of *Carya, Fraxinus* and *Ulmus* of the subclimax and later by *Acer* and *Tilia* of the climax forest, so that the climax comes to replace *Populus* and *Betula* as previously described.

Windthrow areas are to be regarded as miniature clearings. In a *Larix-Picea* swamp in the deciduous forest region when a windthrow occurs, its place is invaded at once by *Larix* and *Picea*, or by *Larix* alone toward the south, which results in keeping the area indefinitely in the same developmental stage. This applies in deep

swamps where *Sphagnum* has developed

In swamps that are more nearly fille
quence, *Sphagnum* makes little or no gr
sometimes *Ulmus* appear in the places l
Cornus stolonifera, Salix discolor and
incana, often come in also, but these are
named above. As the swamp fills up a
comes established, to be succeeded finall
forest, as the process of filling is carried

A *Larix* or *Larix-Picea* swamp, if
by clearing or burning, gradually fills up
ter-content of the soil. With the draini
the filling by washing-in of soil along th
pears. As the filling proceeds, *Larix* d
Ulmus and occasional individuals of *Abi*
ing its place. In that part of the regio
pine forest, *Picea, Abies, Betula* and *Fr*
nants following *Larix* as the swamp bec
filling proceeds, are replaced by *Acer, T*
climax forest. As the result of drainag
introduction of other factors, the normal
Picea associes to the climax *Acer-Tilia* f

The results of the study of successio
tially in accord with the findings of C
(1901), Transeau (1903), Coulter (19
others who have made a study of swam
Illinois, Michigan, Ohio, and eastward to

Cooper (1910) has concluded that on
est is an association of *Abies, Picea* and
as the climax vegetation of parts of nort
and east into Canada. As concerns Mi
not appear to be the case. The *Abies-P*
to be regarded as an associes which ma
initely as a subclimax. Where these tree
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content of the soil too high to permit th
ment of *Pinus*. With the building up of
any other change which would decrease
soil, *Abies, Picea* and *Betula* would und
the *Pinus* association.

swamps where *Sphagnum* has developed abundantly.

In swamps that are more nearly filled up and where in consequence, *Sphagnum* makes little or no growth, *Betula, Populus* and sometimes *Ulmus* appear in the places left vacant by windthrows. *Cornus stolonifera, Salix discolor* and farther northward, *Alnus incana,* often come in also, but these are later replaced by the trees named above. As the swamp fills up a *Populus-Betula* associes becomes established, to be succeeded finally by the climax *Acer-Tilia* forest, as the process of filling is carried still further.

A *Larix* or *Larix-Picea* swamp, if drained and not disturbed by clearing or burning, gradually fills up, thereby reducing the water-content of the soil. With the draining away of the water and the filling by washing-in of soil along the edges, *Sphagnum* disappears. As the filling proceeds, *Larix* dies out, *Populus, Betula, Ulmus* and occasional individuals of *Abies* and *Fraxinus nigra* taking its place. In that part of the region bordering on the climax pine forest, *Picea, Abies, Betula* and *Fraxinus* are the usual dominants following *Larix* as the swamp becomes filled up. These, as filling proceeds, are replaced by *Acer, Tilia* and other trees of the climax forest. As the result of drainage not complicated by the introduction of other factors, the normal succession from the *Larix-Picea* associes to the climax *Acer-Tilia* forest takes place.

The results of the study of succession in Minnesota are essentially in accord with the findings of Cowles (1901), Whitford (1901), Transeau (1903), Coulter (1904), Howe (1910), and others who have made a study of swamps and climax forests in Illinois, Michigan, Ohio, and eastward to Vermont.

Cooper (1910) has concluded that on Isle Royale the climax forest is an association of *Abies, Picea* and *Betula,* and he regards this as the climax vegetation of parts of northern Minnesota and north and east into Canada. As concerns Minnesota at least, this does not appear to be the case. The *Abies-Picea-Betula* stage is rather to be regarded as an associes which may in places persist indefinitely as a subclimax. Where these trees are dominant in Minnesota, the islands or parts of the mainland are low, and the water-content of the soil too high to permit the invasion and establishment of *Pinus*. With the building up of the soil or as a result of any other change which would decrease the water-content of the soil, *Abies, Picea* and *Betula* would undoubtedly be succeeded by the *Pinus* association.

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THE EFFECT OF CERTAIN RUS
SPIRATION OF THE

J. E. WEAVER

Transpiration has long been an inte
ject for investigation. However, in sp
research that has been done on the me
at first independently of the relation to
habitat and more recently with exact
tions of these, a survey of the published
upon the transpiration of diseased plan
ports the results of experiments with
plants of eight different species, of wh
measured for a total of more than 200 i
investigation extended from October, 19
lowing spring.

REVIEW OF PREVIOUS INV

Although it is frequently assumed th
affects the rate of transpiration, there i
perimental data to support this assumptio
an instance of relative transpiration in a
Rubus sp. as compared with a similar b
noconia interstitialis. The branches wer
(on May 24) and immediately placed in
was slightly greater in the healthy speci
were larger than the rusted, but the numb
two specimens. Large test-tubes were u
were left tightly corked over night. Wh
ing of the 25th the healthy branch was
was considerably so. The rusted specim